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THE UNIVERSITY OF ALBERTA

EFFECTS OF PULSE DURATION AND PULSE RATE
ON HUE OF MONOCHROMATIC STIMULI

by



THOMY H. NILSSON

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The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies and
Research, for acceptance, a thesis entitled "Effects
of Pulse Duration and Pulse Rate on Hue of Monochromatic
Stimuli" submitted by Thomy H. Nilsson in partial
fulfillment of the requirements for the degree of
Doctor of Philosophy.

ABSTRACT

It is possible that variations in color are coded in the visual nervous system by the timing of nerve impulses within the color pathways. It has been reported that stimuli of colored light produce changes in brain activity which follow characteristic time patterns depending on the light wavelength. If these temporal patterns of activity mediate color sensations such as hue, disrupting these patterns by appropriate stimulus timing should change the hue sensation produced by the wavelength of that stimulus. Quantitative evidence that such hue changes occur has been reported only recently, but these studies still do not show what aspect of stimulus timing produces the hue changes. More exact knowledge of the stimulus timing conditions which produce hue changes should assist us in determining how the visual system codes color information.

The present study, therefore, was done to determine how the duration or the repetition rate of a stimulus might affect its perceived hue. This was accomplished by having observers adjust the wavelength of light from a steady stimulus until its hue matched that of the light from a stimulus which was pulsed either at certain durations or repetition rates. The difference between the wavelength of the steady and pulsed lights provided a measure of the hue change of the pulsed light. Ten wavelengths from 425 (violet) to 650 (red) nm presented at low and high brightness levels (photopic threshold plus 2 and plus 4 log illuminances) comprised the pulsed light stimuli. Two groups of 4 observers each repeatedly matched the hues produced by these stimuli at 12 pulse durations from 10 to 1000 milliseconds (ms) or at 14 pulse rates from 1 to 37 cycles-per-second (hz).

The results show that various pulse durations or pulse rates produce hue changes which vary in direction and magnitude depending on stimulus wavelength and brightness. At high brightness these hue changes are similar to the Bezold-Brucke effect; while at low brightness a nearly contrary effect was unexpectedly encountered. This discovery suggested a simple explanation for these hue changes. If we consider how the spectral and temporal response characteristics of color pathways are likely to interact at different brightness levels, we can predict the observed hue changes on the basis of overlapping responses in the various types of color pathways at high brightness and on the basis of neural enhancement effects restricted to a single type of color pathway at low brightness. This explanation implies that the low illuminance hue shifts are entirely due to induced changes in the timing of nerve impulses. Further research along this line may reveal the extent to which temporal response characteristics are utilized to code hue information within neural pathways as color is integrated with other perceptual responses in the brain.

APPENDIX A describes an attempt to distinguish within brain activity those effects related to hue sensation from those related to stimulus wavelength by analyzing the cortical potentials evoked by stimuli of various wavelengths and pulse durations.

APPENDIX B describes preliminary measurements of duration hue shifts when the eye has been adapted to various wavelengths of light. These results revealed further evidence that hue is coded within color pathways.

DEDICATION

This dissertation is dedicated to Thomas M. Nelson; mentor, sponsor, friend.

Throughout my graduate studies I have been fortunate to have received the guidance of Thomas M. Nelson, as have many others who showed some willingness to work in perception. Regardless of the field of interest and background of his students, Thomas M. Nelson has patiently tried to cultivate that willingness through his own diverse interests which range from esoteric questions of psychophysics to the mundane relevance of applied psychology. In the present case Thomas M. Nelson encountered a student of uncertain academic standing with a narrow research outlook; he tried to encourage whatever it was he saw in that student. During his tutelage Thomas M. Nelson attempted to teach that student something about the pragmatics of research, but even more he sought to broaden that narrow outlook by demonstrating the richness of research questions which theory can engender and providing opportunities for study in related areas. It is to Thomas M. Nelson I am grateful for whatever success he has achieved with that student.

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This research would not have been possible without the help of many persons both directly and indirectly. But there is one person whose contribution was far greater than that on any other - my wife, Virginia. Not only her work in typing this dissertation with revisions of many of its parts, her objective commentary on the text, and her technical assistance in the lab when no one else was available, do I acknowledge, but in addition to these contributions I am indebted to her for having shouldered more than her share of our other obligations and duties during the course of this study.

The contribution of the observer to perceptual research is perhaps never fully acclaimed. So much of what we have learned and will continue to learn about the mysteries of the human central nervous system rests on the shoulders of those persons who have skillfully and patiently made the often tedious observations which comprise our fundamental data. I was privileged in the present study to have worked with the following observers: Charles Campbell, Carol Cass (L.C.), Millard Evans, Katy Folinsbee, Ann Holmes, Erhart Jeski, Brian MacDonald, and William Olson.

Brian MacDonald provided valuable assistance in setting up and calibrating the optical system. He served as subject for recording visually evoked cortical potentials providing backup data to that reported here.

Erhart Jeski was the very capable assistant with whom I ran the visually evoked cortical potential study. He also helped set up a new vision laboratory in the process.

Alan Nagy assisted in analyzing the visually evoked cortical potential data. He collaborated on

measuring hue and saturation changes under conditions of chromatic adaptation.

While Boring's "Zietgiest" may shape out thoughts and theoretical approach, there is another Zietgiest which is equally as vital in shaping research. This is the technological Zietgiest which provides the wherewithal for carrying out the theoretical dreams. Throughout the course of this study I have been fortunate to receive technical advice and assistance from Paul DeGroot and Patrick Wong. Dennis Jessey and Isao Yamamoto did the excellent machine work required for the spectrum displacement device and the beam chopper.

I thank Stan Rule for his suggestion to look at the variance of the hue shift observations and for his constructive criticism of the text. I am also indebted to Charles Beck for time to run the study while technically working for him.

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INTRODUCTION

Due to significant advances in knowledge of color sensory mechanisms during the past decade, there is emerging a fairly good picture of how spectral information is transmitted to the cortex. At the moment we probably have a more complete picture of afferent color processes than of any other sensory realm. However, we have not yet begun to discover how spectral information, or any other afferent sensory information for that matter, is decoded and utilized to mediate sensory experience. The purpose of this dissertation was to make some inroads into breaking the cortical code for color information.

THE ENIGMA OF COLOR VISION

Young is credited with first recognizing the problem that it was impossible for the visual system to have a different type of receptor mechanism for every color known to man (Gregory, 1966). In vivo measurements of the spectral absorption characteristics of single cones by Brown and Wald (1964) and by Marks, Dobelle, and MacNichol (1964) finally confirmed Young's hypothesis that color vision was mediated by three types of spectral receptor cells: All perceived spectral characteristics of light are synthesized into responses by receptors which are maximally sensitive to light at the wavelength of 450, 530, or 580 nm. While this knowledge solves the problem recognized by Young, it leads to an equally crucial problem - "How are the responses of only three types of receptors analyzed to produce the multitude of hues evoked by various light wavelengths?"

The discovery of four types of spectrally sensitive pathways in the optic nerve by DeValois, Smith, Kitai, and Karoly (1958) means that some analysis already occurs in the retina of the eye to produce four types of spectral sensitivity from three types of receptors: All spectral information relayed to the cortex is transmitted by neurons which are maximally excited or inhibited in an opponent manner by light at approximately 430 and 570 nm or at 520 and 630 nm. Walraven and Bouman (1966) present a theory which suggests how four types of spectral sensitivity are produced by excitatory and inhibitory bipolar cell connections between receptor cells and ganglion nerve cells in the retina.

While it is conceivable that further neural interconnections at the cortical level could result in numerous neurons each having a spectral responsiveness as narrow as color difference thresholds, this seems unlikely. Andersen, Buchman, and Lennox-Buctal (1962) and Motokawa, Taira, and Okuda (1962) found cortical cells whose spectral sensitivities were somewhat narrower than the spectral-opponent ganglion cells of the retina or lateral geniculate, but subsequent researchers (Gouras, 1970; Massopust, Wolin, and Kodoya, 1969) have not found evidence of cortical cells whose peak sensitivity is significantly different from those in the optic nerve. This is not too surprising since a single-cell-single-hue spectral analysis code would be an extremely inefficient way to produce color vision.

EVIDENCE FOR A TEMPORAL COLOR CODE

There is evidence which suggests that the spectral characteristics of light may be coded at the cortex

by a method which is rather different from that requiring individual cells for each color. Ingvar (1959), Shipley, Jones, and Fry (1965) and Ciganek and Ingvar (1969) reported that stimuli of different wavelengths produce discrete temporal patterns of cortical activity. Fourier analysis by Shipley, Jones, and Fry (1968) of spectral evoked cortical potentials revealed frequency components which vary as a function of stimulus wavelength. These physiological data suggest that wavelength may be coded in terms of a temporal rather than structural code at the cortical level. Suggestions that color may involve a temporal as well as a structural code in the visual system have been proposed repeatedly (Troland, 1933; Fry, 1945; Talbot, 1951; Ingvar, 1959; Ikeda and Boynton, 1962; Shipley, et al., 1968; Nelson, 1971), but as yet we lack definitive evidence implicating temporal response with sensory effect.

If the temporal patterns of activity observed by Shipley and others at the cortex reflect processes which mediate the perception of color, one might expect that altering the temporal characteristics of spectral stimuli would alter their hue since temporal alternations of stimuli are known to alter the temporal patterns of their evoked cortical activity (Canter & Fleming, 1966; Regan, 1970; Wicke, Donchin, and Lindsley, 1964). However, until recently there was no quantitative evidence of whether variation in the temporal parameter of a spectral stimulus altered the perceived hue of that stimulus.

While the temporal induction of hue in white light is a well known phenomenon, such hue effects have generally been attributed to differences in

threshold rise times (Campenhauser, 1969) or in lateral interactions (Brown, 1965) which selectively favor some color mechanisms. Since white light can stimulate all color mechanisms, these temporal induction phenomena do not appear to demonstrate that color may be temporally coded as much as they demonstrate that certain color mechanisms enjoy an advantage over others under certain patterns of stimulation.

An early report that monochromatic stimuli might be temporally altered in hue was made by Fry (1936). Fry reported on the color impressions produced when various wavelengths of light were flickered at several frequencies. Though Fry concludes that "the hue of the bright flashes (as opposed to dark intervals) was characteristic of the wave-length", his data gives evidence that some changes in the hue of the flashes was also noticed. Definite reports that flickering spectral stimuli change in hue were subsequently made by Christian, Hass, and Weizacker (1948); Bartley and Nelson (1960); Ball (1964); and Bleck and Craig (1965). These studies relied mainly on subjective reports of any hue shifts and did not produce any quantitative data on the phenomenon. The fact that they also differed greatly as to method and reported conflicting results left the question of temporally induced hue shifts undefined and largely unnoticed.

Quantitative hue measurements of flickering stimuli were first made by Horst and Muis (1969) and Nilsson and Nelson (1971). In these studies stimulus wavelength was controlled by means of a monochromator and observers adjusted the wavelength of a second monochromatic beam to match the hue of the flickering stimulus. This method permitted measuring hue shifts in terms of the difference in wavelength between flickering and matching stimuli. The results were that altering the temporal characteristics of monochromatic stimuli produced measureable hue changes which definitely extend beyond

the hues normally produced by the incident wavelengths. These results suggest that temporal hue shifts are the result of a previously undetermined relation between the temporal characteristics of spectral stimuli and their perceived hue.

BREAKING THE CODE FOR HUE

The finding that hue can be altered by altering a stimuli's temporal parameter and the possibility that hue may be temporally rather than structurally coded, presents what is possibly a unique opportunity to learn how stimulus information is processed to produce a sensory effect.

Changes in the temporal response of the central visual system are the only changes which at present can be studied in detail under normal conditions with humans. It follows that temporal qualities of sensory effects would therefore be the first to be definable in terms of cortical processes, and as mentioned earlier (Canter & Fleming, 1966; Regan, 1970; Wicke, et al., 1964) significant progress has been made in this direction. The visual system seems poorly adapted, however, to conveying purely temporal aspects of stimulation. Studies such as those by Bartley and Wilkinson (1953) and by Kietzman and Sutton (1968) have found that even the simplest temporal discrimination, temporal acuity, is subjectively an ephemeral phenomenon the measurement of which may be dependent on the means used to obtain that measurement. It appears that the temporal aspects of visual stimulation are more normally integrated with other parameters of the stimuli to produce sensory effects such as brightness or motion.

On the other hand, while the hue qualities of sensation are pervasive in most photopic perceptions, they retain prominent attributes which are directly

traceable to the stimulus parameter of wavelength. Unlike temporal discriminations, hue is readily observable and measureable. With temporal hue shifts we have a means of altering hue independently of wavelength by introducing only a temporal change in the stimulus. The effects of this temporal change should be observable at the cortical level, and thereby permit determination of what cortical responses are related to a sensory effect, hue, as opposed to a stimulus parameter, wavelength.

It should therefore be possible to break a temporal code for hue by means of the following steps: 1) Establishing exactly which temporal parameter of monochromatic stimulation produces hue shifts and measuring these shifts. 2) Recording the cortical responses evoked by monochromatic stimuli under conditions which do and do not produce hue shifts. 3) Determining which cortical response characteristics are common to stimuli of different wavelength but of the same apparent hue. 4) Checking these characteristics in stimuli having similar hue but differing in various other parameters such as size or shape.

AN ANALYTIC KEY TO PERCEPTUAL PROCESSES

Discovery of how hue is coded at the cortex would represent a breakthrough in understanding how sensory effects are mediated. Once we have broken the code for one attribute of sensation, it should be possible to use this code as an analytic key to other perceptual responses, even those which are spatially coded and generally indiscernable by present recording methods.

For example, it has been postulated that form perception is a multi-stage process developing

from an integration of elemental responses to brightness, contour, etc. (Flavell & Dragnus, 1957; Vernon, 1952). Physiological recording from single cortical cells in animals (Campbell, Cooper, and Enroth-Cugell, 1969; Hubel & Wiesel, 1965) reveal what are probably early stages in the process of contour detection, and psychological studies such as by Blakemore and Campbell, (1969) and Graham and Nachmias (1971) are substantiating the relevance of these findings to human perception. But as pointed out by Hubel (1963), we can still only speculate on developments beyond these early stages.

A study by Bouma and Andriessen (1968) together with one by Held and Shattuck (1971) suggest one avenue by which knowledge of the cortical response code for hue could be utilized to trace further stages in the development of form perception. Bouma and Andriessen observed that the accuracy of perceived line orientation varied with line angle in a manner similar to variation in the relative number of simple receptive field cells specifically sensitive to stimulus angle as found by Pettigrew, Nikara and Bishop (1968) in the cortex. Held and Shattuck found the tilt after-effect of perceived line orientation was hue dependent. These studies together indicate that early stages of angle detection in humans are similar to what has been observed in animals and that information at these stages is hue specific. This suggests that a knowledge of the cortical code for hue could be used to trace responses involved in form perception at least to those stages following simple receptive fields by using colored stimuli varying in complexity from single lines at various angles, to pairs of intersecting lines, and finally to enclosed forms.

A second method to use the cortical code for

color to study form perception would utilize a phenomenon first observed by Helson and Fehrer (1932). They noted that as the viewing duration of simple forms was increased from zero, the appearance of form gradually gained certain features such as brightness and edge as opposed to the form appearing all at once. By using as stimuli forms having various characteristics such as contour, angle of edges, and enclosure in different colors it might be possible to discern the development of these features at the cortical level as duration is increased.

AIMS OF THE PRESENT STUDY

The following is a report of research directed towards breaking the cortical code for color vision. The main part describes an experiment which sought to determine what stimulus parameters were producing the intermittency hue shifts observed in previous studies.

Research by Horst and Muis (1969) and Nilsson and Nelson (1971) has established that changes in temporal characteristics of a monochromatic stimulus can produce measurable changes in its perceived hue. The results of these studies indicate that temporally induced hue shifts should not be confused with the Bezold-Brucke hue shifts which accompany changes in stimulus illuminance. While these studies showed that temporal hue shifts differ in magnitude and direction from illuminance hue shifts, they did not establish what temporal parameter actually is producing these shifts. Because both studies used flickering stimuli produced by an episcotister, one cannot determine if the effects of flicker frequency on hue are due to changes in pulse duration or changes in pulse rate as flicker frequency is changed. Investigation of

the possibility that flicker hue shifts arise from some intrinsic temporal coding of color requires more exact data on the stimulus conditions which temporally induce hue shifts. The present study sought to determine what hue changes occur as pulse duration or pulse rate are varied and whether these hue changes are affected by illuminance.

While further clarification of the flicker hue shift phenomenon itself was called for, it also appeared that there has been little previous quantitative study of changes in hue with change in the duration or pulse rate of a spectral stimulus. Changes in brightness and saturation of spectral stimuli with change in duration have been reported by Ikeda and Boynton (1962), Jameson and Hurvich (1962), Kinney (1965), Stainton (1928), Troland (1930), and Wasserman (1966). In some of these studies hue changes were noted but only Kinney (1965) measured hue changes. Kinney used a colorimeter to match the appearance of 50 to 400 ms duration pulses of broad-band stimuli; the only notable hue shifts were those of red stimuli shifting towards yellow as duration was decreased. The effect of duration on hue has been studied using color naming techniques (Luria, 1967; Weitzman and Kinney, 1969). Luria's results suggest that as duration is decreased blue stimuli become bluer and green stimuli shift towards yellow at both 0.15 and 15 ft L luminances, while red shifts towards yellow only at the higher illuminance. Weitzman and Kinney (1969) found that green stimuli shift towards blue and that yellow shift towards red with decreasing duration, though their study used stimuli of small visual angle to induce partial foveal tritanopia. These color naming studies also suggest that duration hue shifts may vary with stimulus illuminance and area.

There appears to be no previous study of the

effects of pulse rate on hue. But the possible existence of duration hue shifts meant that the measurements in previous flicker studies represent an interaction between hue shifts accompanying the changes in duration and a still undetermined effect due to pulse rate.

PURSuing COLOR RESPONSES AT THE CORTEX

An initial attempt was also made to determine what characteristics of evoked cortical responses are related to hue. Evoked cortical potentials were obtained for spectral stimuli of various durations similar to those for which hue shifts were measured in the main part of this report. Subsequent study of the evoked potential waveforms was done using specific component analysis, Fourier analysis, and cross-correlation analysis. These analyses all showed that the visually evoked cortical responses varied with stimulus wavelength, duration, and illuminance but these variations were not systematic. The failure to find a systematic relation for wavelength or hue is believed to be due to the large day to day variability encountered with the recording techniques. A more complete description of this experiment is included in APPENDIX A.

The significance of the evoked potential experiment lies mainly in that it served to develop the recording and data analysis techniques to be used in future studies. The results also showed that the temporal pattern of cortical responses to stimuli of different wavelength varied with stimulus duration. This would be expected if a temporal code was involved in the hue shift phenomena, and the effect has probably not been looked for previously.

However, it is also to be expected that whenever the conditions of stimulation are changed in some manner, one should be able to detect a difference somewhere in the visual system with sufficiently careful measurements. The lack of more unequivocal results of the experiment raises the possibility that initial detection of changes at the cortical level related to hue changes of only around 10 nm might prove difficult even with more controlled techniques. This realization led to a search for conditions under which the temporal hue shift effect might be further enhanced.

FURTHER EVIDENCE OF INTRANEURAL COLOR CODING

The possibility was considered that the limited extent of the temporal hue shifts observed up till now might be due to the confounding effect of simultaneous hue shifts in various color pathways. For example, a stimulus at 475 nm might temporally induce a hue shift towards deeper blue in the blue pathways, but the blue pathways are not the only ones stimulated by this wavelength. If the green pathways stimulated by this wavelength were affected in a manner also leading to a hue shift towards blue in the green pathways, the difference between the responses in blue and green pathways would be decreased and the composite result could be a smaller hue shift of the 475 nm stimulus than its effect on either pathway alone. This suggested that larger hue shifts might be produced if the stimulus effects could be restricted to single color pathways.

If it is postulated that temporal hue shifts are the result of induced changes in the response patterns of color pathways, it follows that it should be possible to change the hue effect produced by a

given pathway independently of other pathways - i.e., it should be possible to make a normally green 525 nm stimulus appear bluer by changing only the response of the green color pathways and without involving the response of the blue pathways. This hypothesis could be tested by measuring hue shifts under various conditions of chromatic adaptation - i.e., by "knocking out" the blue pathways using a 450 nm adapting stimulus and measuring the hue shifts of 525 nm stimuli under conditions where these otherwise shift in hue towards blue. If under such conditions the stimuli can still shift in hue towards the adapting wavelength, one would have further evidence that hue is coded within as well as between the color pathways. As pointed out above, such a procedure might also result in the appearance of much larger hue shifts, an effect which could facilitate discerning the code for hue at the cortical level.

Preliminary observations have been made of temporal hue shifts under conditions of chromatic adaptation. A brief description of this experiment is reported in APPENDIX B pending a more complete study in progress. The results of these preliminary observations indicate that: 1) Brief durations of spectral stimuli can induce hue shifts towards the hue of the adapting wavelength. 2) These hue shifts are much larger than those observed under nonadapted conditions. These results look promising not only in supporting a theory of temporal coding of hue within color pathways, but also for indicating conditions which might facilitate breaking the code for hue at the cortical level.

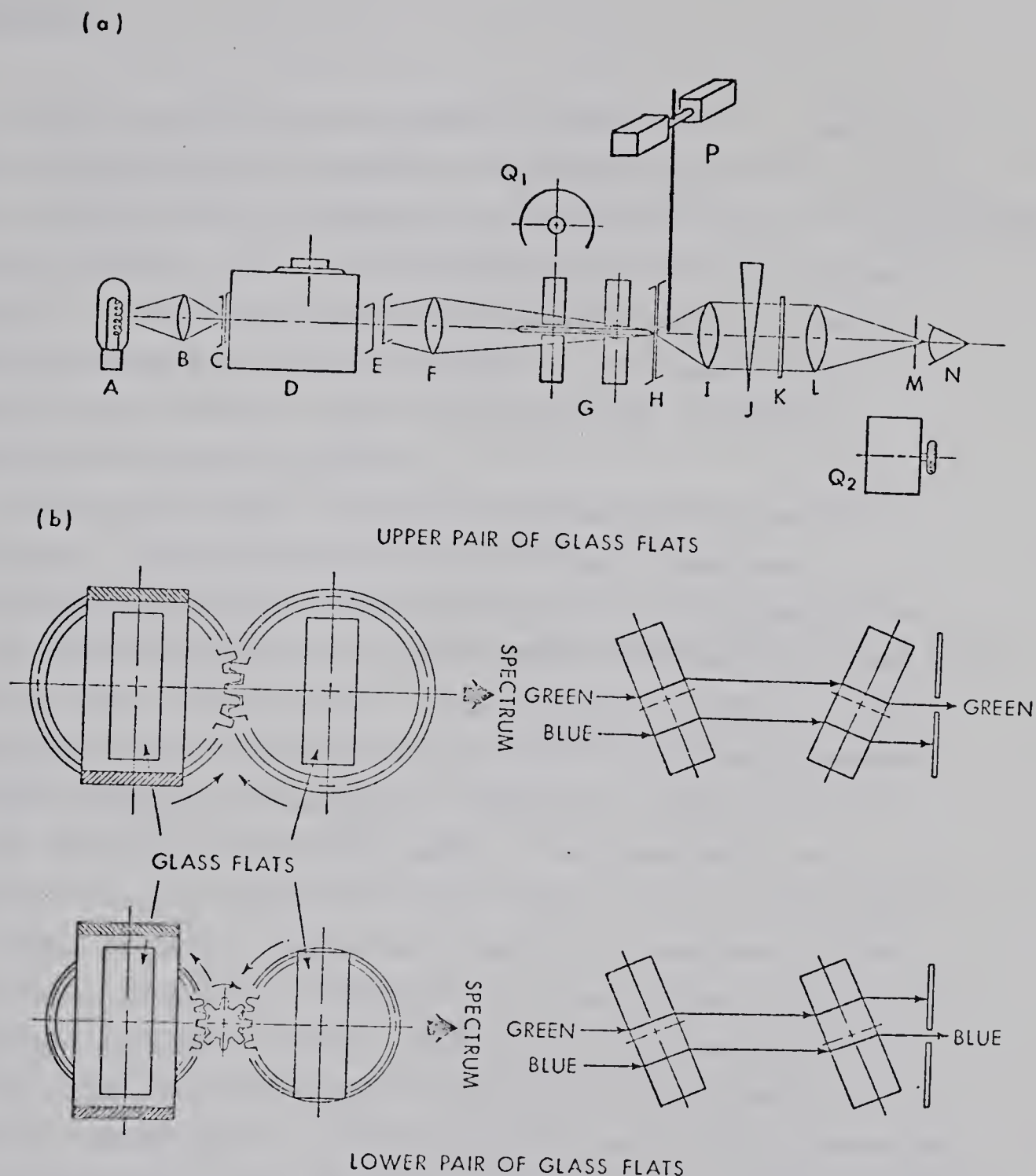


Fig. 1. Apparatus.

- a) Side view schematic diagram of the optical system: A-E, monochromator and tungsten light source; F, condenser lens; G, spectrum displacement device; H, exit slit; I-L, viewing optics; M, artificial pupil; N, observer; P, beam chopper; Q_1 and Q_2 , Selsyn motors.
- b) Top view diagram showing principle of the spectrum displacement device: As flats are rotated, refraction displaces spectrum passing through the lower pair.

METHOD

OBSERVERS

Eight persons were hired as observers. Seven were undergraduate students in psychology with little prior experience in making any psychophysical observations. A staff member, W.O., was experienced at making hue matches. All were naive concerning temporal and Bezöld-Brücke hue shift effects. All observers demonstrated normal color vision using Ishihara pseudoisochromatic plates.

Each person was initially given five practice sessions. During the first of these sessions preliminary photopic thresholds were established for steady presentation of each of the wavelengths, and the observer was introduced to making hue matches. The subsequent four sessions were run in the same manner as experimental sessions to allow the observers to become familiar with the task. No feedback of results was provided until the end of the experiment.

Four persons observed stimuli of various pulse durations, and four observed various pulse rates. In the pulse duration group, observer B.M. matched 8, K.F. 6, W.O. 6, and A.H. 5 replications of each stimulus condition. In the pulse rate group observer C.C. matched 6, M.E. 6, E.J. 5, and L.C. 4 replications.

APPARATUS

The apparatus was similar to that used by Nilsson and Nelson (1971) and is shown in Fig. 1-a. It comprised a Bausch and Lomb "Hi Intensity" grating monochromator model #2 with a 45 watt tungsten quartz-iodine light source and an achromatic condenser

lens, a spectrum displacement device, an electromechanical beam chopper, and viewing microscope optics. The viewing optics consisted of a 38 mm focal length Erfle lens which collected the light emerging from the exit slit of the spectrum displacement device and a 90 mm focal length Leitz colourplan lens which focused that exit slit at the retina with an approximately 2.5x magnification. This optical apparatus presented the observer with two monochromatic stimuli. The temporal parameter of one stimulus was defined by the test condition; its wavelength was set by the experimenter. The other stimulus was on steadily; its wavelength could be adjusted by the observer to match the hue of the test stimulus.

The spectrum displacement device converted the output of the single monochromator into two beams. By means of optical flats which could be adjusted to various angles with respect to the monochromator spectrum, this device could produce a wavelength change in one beam as is shown in Fig. 1-b. The device is describe elsewhere in greater detail (Nilsson, 1971).

The essential difference in the present apparatus was the replacement of Nilsson and Nelson's (1971) episcotister with a beam chopper. The beam chopper enabled independent control of pulse duration and repetition rate of the test stimulus. It consisted of a pendulum type shutter mounted in front of the exit slit of the spectrum displacement device. The shutter was pulled by two opponent General Electric model 4-DC-2-C-24 solenoids operated at 24 VDC. These solenoids were driven through a flip-flop type electronic switch. A series of electronic timers (Nilsson, 1969) controlled the pulse sequencing. Light pulses were monitored on line by an RCA IP21

photomultiplier with an oscilloscope display. Light pulses produced by this device had 90 percent rise and fall times of less than 2 ms. The device could produce pulse rates from 0 to 50 Hz without interference from mechanical resonance.

Observations were made from a light tight, sound deadened, ventilated booth. A 4 mm artificial pupil was used, and head position was maintained by a bite-board system. Maximum illuminance of the system at 575 nm was 7.5 lu/cm^2 as measured at the position of the pupil. Illuminance was controlled in both beams by means of a Kodak Inconel neutral density wedge and Tiffen neutral density filters. A 1.5 mm exit slit on the monochromator resulted in a 5 nm half-intensity-band-width of the stimuli. The view consisted of two rectangular fields, the test and the match stimuli, positioned one above the other. These stimuli each subtended a visual angle of $2^\circ 30'$ in height and $1^\circ 14'$ in width; they had a separation of $45'$.

PROCEDURE

After the practice sessions, photopic thresholds were again determined for steady presentations of each stimulus wavelength with each observer using the method of limits. Stimulus illuminance levels of 2 and 4 log units above the steady stimulus photopic threshold were presented on alternate days. Hue shifts were tested at ten wavelengths: 425, 450, 475, 500, 525, 550, 575, 600, 625, and 650 nm. Hue shift was measured as the difference between the wavelength of the test stimulus and the wavelength of the match stimulus as adjusted by the observer to obtain a hue similar to that of the test stimulus.

Since the observer could only vary the wavelength of the matching stimulus, he was instructed to try to ignore any differences in brightness and saturation of the test and matching stimuli and to select the best match possible on the basis of hue alone.

The dark adapted observer matched hues at each wavelength for a given pulse duration or pulse rate of the test stimulus, and then duration or rate was changed. Wavelengths and durations or rates were presented in ascending and descending orders, which were scrambled and equated across sessions.

Eleven pulse durations of 10, 20, 40, 60, 80, 100, 120, 140, 160, 200, and 1000 ms plus a control condition with a steady stimulus were used. For this set of conditions pulses were presented with a 2 sec interval between the offset of one pulse and the onset of the next pulse. Alternate pulse durations were presented on alternate days to keep the length of these sessions down to about an hour. Depending on the observer a total of from 5 to 8 matches was made at each illuminance x duration x wavelength condition.

Thirteen pulse rates of 1, 3, 5, 7, 9, 11, 13, 15, 17, 21, 25, 31, and 37 Hz plus a control condition with a steady stimulus were used. The pulse duration was always 10 ms. Alternate pulse rates were presented on alternate days to keep the length of these sessions down to about an hour. Depending on the observer a total of from 4 to 6 matches was made at each illuminance x rate x wavelength condition.

Table 1. Hue shifts in nm produced by various pulse durations of monochromatic stimuli at an illuminance of threshold plus 2 log; average of repeated matches by each observer, and pooled average standard deviation of matches.

PULSE DUR. (ms)	STIMULUS WAVELENGTH (nm)										OBS. & s.d.
	425	450	475	500	525	550	575	600	625	650	
10	-14.1	-9	-2.6	-5.7	-9.7	-1.8	6.6	7.4	13.1	22.9	B.M.
	-10.7	-12.8	-3.5	-5	-12.6	-0.3	5.4	3.5	4.3	11.5	K.F.
	-8.1	-9.2	8.2	-2.7	-4.7	0.2	3	7.1	17.8	22.6	W.O.
	-6.3	-11.6	0.5	-3.8	-12	1.2	4.7	2.6	4.3	3.4	A.H.
	3.4	3.2	4.4	2.2	7.1	6	3	3	7	10.9	SD
20	-10.4	-8	1.1	-2.6	-7.5	-0.6	3.9	3.8	18.8	18.9	B.M.
	-6.7	-9.5	0.3	-3.4	-7.5	3.2	5.9	3.2	4.8	13.5	K.F.
	-7.8	-5.7	0.3	-2.1	2	2.1	0.3	4	16.7	22.2	W.O.
	-8.4	-11.1	1.5	-2.3	-13.5	2	4	1.3	4.6	6.5	A.H.
	2.9	3.1	3.8	2.7	3.9	3.9	1.8	2.4	6.9	10.3	SD
40	-6.2	-1.3	-2.1	0.6	3	3.5	0.7	-1.5	-4.4	18.1	B.M.
	-5.4	-6.7	-1.7	0.4	1.5	7.1	2.3	-1.2	-1.6	0.3	K.F.
	-2.2	0	4.2	-2.3	8.2	4.4	0.1	1.2	6.3	17.7	W.O.
	-5.1	-7.9	0.4	-1.2	1.6	6.7	3.1	0.1	4.4	8.6	A.H.
	2.9	3.1	1.9	1.6	3.7	3	2.3	2.5	4	6.1	SD
60	-6.6	-3.4	1.3	1.4	3.6	3.9	1.1	0.7	2.3	19.3	B.M.
	-4.1	-1.5	0.6	0.4	5	5	3.5	3.3	1.9	0.1	K.F.
	-3.4	-1.7	3.7	3.8	7.3	5	0.4	0.9	6.3	14.8	W.O.
	-2	-3.7	-0.6	0.1	5	5.6	2.1	0.5	4.8	10.8	A.H.
	3	3.3	1.8	1.9	4.2	2.3	1.9	3.4	4.2	5.4	SD
80	-4	-0.6	2.6	3.8	5.7	5.6	0.6	-0.1	0.8	18.1	B.M.
	-5.4	-5.1	-0.9	0.9	6.5	5.3	1.4	-0.5	-4.4	4.7	K.F.
	-2	-3.2	2.8	2.9	9.3	5.4	1.1	-1.2	3	10.8	W.O.
	-0.8	-4.4	-0.1	0.2	10.5	7	1.4	-1.1	2.8	3.3	A.H.
	3.4	3.2	1.3	1.6	2.5	2.2	0.9	1.5	4.7	5.2	SD
100	-4.1	-2.7	1.5	2.1	5.5	4.3	0.8	0.2	1.9	17.3	B.M.
	-3.1	-2.5	1.5	0.8	6.3	3.5	2.8	1.1	-2.7	4.1	K.F.
	-1.4	0	2.8	1.8	2.6	3.4	0.8	0.6	3.5	13.2	W.O.
	0	-0.4	0.5	1.4	6.1	4.7	2.3	0.7	4.2	7	A.H.
	1.8	3.4	2.6	1.4	3.8	3.5	1.4	1.7	4.1	6.7	SD
120	-2.5	-1.2	1.5	3.2	5.9	4.8	0.3	-0.2	1	17.4	B.M.
	-3	-1.6	0.9	1.4	5.2	6.3	3.2	-0.2	-3.8	7.7	K.F.
	-0.6	-5	1.6	3.1	5.4	5.6	1.9	1.4	5.1	7.9	W.O.
	-0.5	-1.3	0	1	9.9	5.3	1.9	-0.4	1.4	6.6	A.H.
	2.2	3	1.9	2.3	3	2.2	1.4	1.3	3	6.5	SD
140	-3.1	-2.3	1.3	2.6	4.8	2.9	1.1	-0.4	-3.6	15.5	B.M.
	-1	-0.3	1.1	1.3	5.2	4.3	3.1	-0.1	-2.7	6.2	K.F.
	-1.6	-0.7	2.3	2.8	6.2	5.2	1.6	-2.4	6.6	18.3	W.O.
	-0.2	-1.6	-1.5	2.1	7	5.4	1.6	-0.2	0.6	8.1	A.H.
	1.4	2.6	0.9	1.7	2.6	2.1	1.4	1.6	3.3	6.6	SD
160	-1.1	-2.8	1.6	3.5	4.1	4.1	1.2	-0.1	-0.2	18.3	B.M.
	-0.9	-0.2	-0.8	1.3	6.4	4.1	2.9	-0.4	-3.9	4.6	K.F.
	-1.7	2.3	1.9	3.3	4.2	3.3	1.6	2.8	3.5	6.8	W.O.
	-0.9	2.1	0.2	1.6	5	3.9	1	0.6	1.1	2.7	A.H.
	1.6	3.9	1.4	1.9	3	2	1	1.6	3.3	8.1	SD
200	-2.5	-0.7	1.4	2	2.1	2.3	1.4	0.4	-5.4	16.1	B.M.
	-1.2	-1.4	1.1	0.2	1.9	0	2.7	1.5	-1.2	5.2	K.F.
	0.5	2.8	1.8	3.3	3	2.2	2.3	4	10.8	16.3	W.O.
	0.9	1.9	-0.1	1.2	4.3	3.7	2.2	1.5	3.1	6.2	A.H.
	1.3	3.4	1.5	1.6	3.1	2.5	1.3	2	4	8.9	SD
1000	-0.6	2.3	1.6	1.4	1.2	0.5	0.6	-0.8	-3.4	-5.9	B.M.
	0.6	0.9	0.3	1.9	3.1	1.8	1.6	1.2	0	-2.7	K.F.
	1	3.8	3	3.3	2.4	1.3	2.3	2.8	3.8	1.3	W.O.
	0.2	1.7	0.7	1.7	3.6	2.5	1.9	1.7	0.5	0.5	A.H.
	0.9	3.1	1.1	1.1	1.9	1.3	0.7	1.2	2.3	4.8	SD
STEADY	0.3	1.2	0.1	-0.3	1	0.8	-0.6	-1.2	-2	-1.7	B.M.
	0.4	1.4	0.4	1.3	0.4	0.6	0.6	-0.7	-3.2	-5.3	K.F.
	0.5	1.7	2.1	1.8	2.4	0.8	1	1.1	0.1	1.3	W.O.
	0.7	1.7	0.9	1.9	3.6	2.7	0.8	-0.3	-1.1	-3.9	A.H.
	0.6	2.6	0.8	0.7	1.1	0.8	0.5	1.1	1.9	6.2	SD

Table 2. Hue shifts in nm produced by various pulse durations of monochromatic stimuli at an illuminance of threshold plus 4 log; average of repeated matches by each observer, and pooled average standard deviation of matches.

PULSE DUR. (ms)	STIMULUS WAVELENGTH (nm)										OBS. & s.d.
	425	450	475	500	525	550	575	600	625	650	
10	-4	-9.2	-1.6	5.8	16.4	8.8	0.8	-1.4	10.6	20.6	B.M.
	-4.5	-7.8	-2.3	5.9	18.3	11.8	3.5	-1.3	-7.8	-8.3	K.F.
	-4.8	-9.2	-7.1	-0.7	8.7	4.8	-1.5	-1.5	-0.9	5.6	W.O.
	-7.7	-13.3	1	-1.3	20.5	14.3	2.7	-2.9	-5.9	14.9	A.H.
	4.2	4.3	9.4	4.9	4.9	4.6	2.4	2.9	6.3	11	SD
20	-3.7	-10.5	-2.3	2.6	6.8	5.3	0.7	-2.7	-2.2	17.1	B.M.
	-5.5	-10.2	-4.4	0.4	13.3	13.7	6	-0.8	-7.5	-17	K.F.
	-3.1	8.5	-10	2.8	2.1	2.8	0.8	-2.4	-2.4	7.4	W.O.
	-6.8	-16.2	-1.5	1.3	12.5	14.4	3	-4.4	-9.5	3	A.H.
	4.5	4.4	9.8	3.1	7	2.9	3	2	6.2	9.8	SD
40	-5.8	-12.9	-8.1	1.1	6.4	7.1	3	-0.7	-4.1	-1.9	B.M.
	-7.1	-11.5	-5.4	0.3	19	10.6	3.8	0.4	-9.2	-15.5	K.F.
	-4.8	-9.3	-4.3	1.6	0.8	3	0.8	-1.7	-1.6	6.4	W.O.
	-8.4	-16.3	7.5	-0.2	17.5	12.5	3.2	-6.8	-13.8	-11.5	A.H.
	3.5	4	8.3	2.7	5.6	2.9	2.5	2	3.5	9.2	SD
60	-3.7	-9.6	0.9	-0.3	2.1	3.3	2.4	0	-5.4	-6.9	B.M.
	-8.3	-5.8	-1.7	0.5	7.4	10.6	6.3	-0.7	-3.6	-12.7	K.F.
	-2.7	-4	-1.1	5.4	1.2	5	2.9	-0.7	1	6.1	W.O.
	-5.1	-10	5.3	-0.1	12	12.2	1.3	-4.1	-9.2	-6.6	A.H.
	2.7	7.6	6.1	2.7	6.3	3.2	3.2	2	5.2	10	SD
80	-1	-8.7	-0.1	2.3	3.9	3.6	3.5	1.5	-1.4	-2.1	B.M.
	-6.1	-6.7	-3.2	0.1	6.1	7.8	4.2	0	-4.8	-9.2	K.F.
	-5	-3.7	0.2	-3.3	-1	2.3	0.3	-0.2	-0.7	9.7	W.O.
	-5.8	-15.9	7.4	-0.9	12.4	7.4	1.1	-5.1	-10.5	-14.5	A.H.
	4	5.7	3.5	2.1	4	3.6	2.4	1.9	3.3	5.7	SD
100	-2.4	-3.4	-2.4	-0.9	2.2	3.4	2.3	0.6	-1.2	-4	B.M.
	-6.2	-4	0.8	-0.4	3.3	5.7	5.3	2.8	-1.9	-2.7	K.F.
	-0.9	-3.7	-2.3	-4.4	0.8	6.3	2.6	0	0.2	7.3	W.O.
	-4.1	-14.6	-2.9	-1.5	0.1	10.2	3.4	-3	-5.7	-3.1	A.H.
	2.2	5	6.2	2	5.4	3.8	2.2	2.3	3.3	5	SD
120	-0.9	-0.9	0	-0.7	0.8	1.9	2.6	2.8	-0.6	-3.4	B.M.
	-6.8	-4.8	-1.7	-0.7	0.8	4.1	3.3	1.4	-1.2	-1.6	K.F.
	-4.3	-4.8	-2.2	2.8	1	2.3	0.8	-0.7	0.3	9	W.O.
	-3.5	-6.2	0.1	-3.4	5	5.8	0.7	-4.3	-7.7	-9.6	A.H.
	3.5	8.3	4.7	1.9	4.4	2.5	1.7	2.4	4.1	5.8	SD
140	-0.1	9.7	-0.9	-0.1	-1.4	1.3	1.9	1.1	-1.7	-2	B.M.
	-3.7	-1.7	0.3	-0.4	1.6	4.9	4.6	1.6	0.8	3.7	K.F.
	0.9	-0.7	1.3	-4.2	2.1	5.2	2.8	0.3	0.5	11.1	W.O.
	-0.1	3.8	0.8	-2	-3.2	6.5	1.9	-1.2	-4.6	-2	A.H.
	1.4	7.9	4	2.1	3	3.4	1.6	2.1	2.5	7.3	SD
160	-0.1	6.2	-1.5	-0.4	-0.3	0.4	1.8	1.8	-1.4	-2.9	B.M.
	-0.6	0.2	-1.2	-0.1	2.8	2.8	4.1	2.3	1.3	2.3	K.F.
	1.8	-4.8	-1.2	-2.6	0.3	2.1	0.8	0.9	2.3	9.5	W.O.
	-2.6	-1	-2.6	-2.2	1.4	2.5	0.5	-3	-2.1	-8.9	A.H.
	3	9.2	3.5	2	3.5	2.3	2.2	1.4	3.3	5.9	SD
200	0.6	12.1	1.4	-0.5	-1.2	1.4	1.2	1.9	-0.4	-1.4	B.M.
	-1.5	2.7	-1.3	-0.6	2.3	3.8	1.7	2.4	-0.4	-1	K.F.
	0.8	4.8	-0.2	-4.8	-2.8	4.3	2.8	2.8	4.3	9.8	W.O.
	0.6	0.5	1.3	-0.8	-1.6	3.1	1.6	-1.4	-2.3	-2.3	A.H.
	2.6	8.1	4.5	1.8	3.7	3.5	2.3	2.2	3.4	6.1	SD
1000	0.4	6.4	0.7	-0.4	-0.7	0.6	0.3	0.1	-1.9	-0.4	B.M.
	-0.3	3.3	0.1	0.1	-0.1	0.4	1	0.8	-0.5	-1.4	K.F.
	0.8	7.7	3.2	2.7	3.1	3.7	0.3	1.3	-0.4	-1.1	W.O.
	0.7	8.5	2.1	0	0.4	0.8	-0.3	-0.4	-3	-3.6	A.H.
	0.9	4.1	2.8	1.1	2	1.3	1.4	0.8	2	4.8	SD
STEADY	-0.4	-1.7	-1.8	-0.3	0	0.2	-0.6	-0.6	-2.3	-4.1	B.M.
	-1.2	-2.2	-0.7	0	-0.3	-0.5	-0.1	-0.1	-0.7	-0.1	K.F.
	-1.7	0.8	-0.4	-1.3	0.5	-0.3	-0.1	-1.5	0.9	-0.4	W.O.
	0	2.6	1.8	-0.2	0.3	0.4	-0.6	-0.4	-5.1	-8.7	A.H.
	0.8	4.3	1.6	0.2	0.6	0.9	0.7	1.3	1.3	3.3	SD

RESULTS

Because hue shifts were measured as the wavelength difference between test and matching stimuli, the results are presented as positive and negative wavelength numbers depending on whether the matches were of a longer (positive) or shorter (negative) wavelength than the test stimulus. For example, a hue shift result of -10 nm at a test stimulus wavelength of 550 nm means that the observer adjusted the matching stimulus to a wavelength of 540 nm.

In the tables, the observers are listed in order of the number of matches upon which their averaged results were based. Interobserver variability is evident in these tables by differences between observers in their average matching wavelength. Intraobserver variability is indicated by the standard deviation obtained from the pooled variance of the matches by each observer. Since the interobserver variability is generally similar to the intraobserver variability, and since all observers except one had little prior experience in tasks of this nature, the results are graphically represented in terms of the average of all matches by all observers of a given stimulus condition.

PULSE DURATION

The effects of pulse duration on hue at illuminance levels of threshold plus 2 and 4 log units are shown in Tables 1 and 2. Observer variance at shorter durations of the 625 and 650 nm stimuli was notable greater than for other conditions and includes significant reversals in hue shift direction. This variability was probably due to variations in observer criteria with respect to the edge effects discussed by Nilsson and Nelson (1971) and also due to the difficulty of ignoring considerable desaturation at

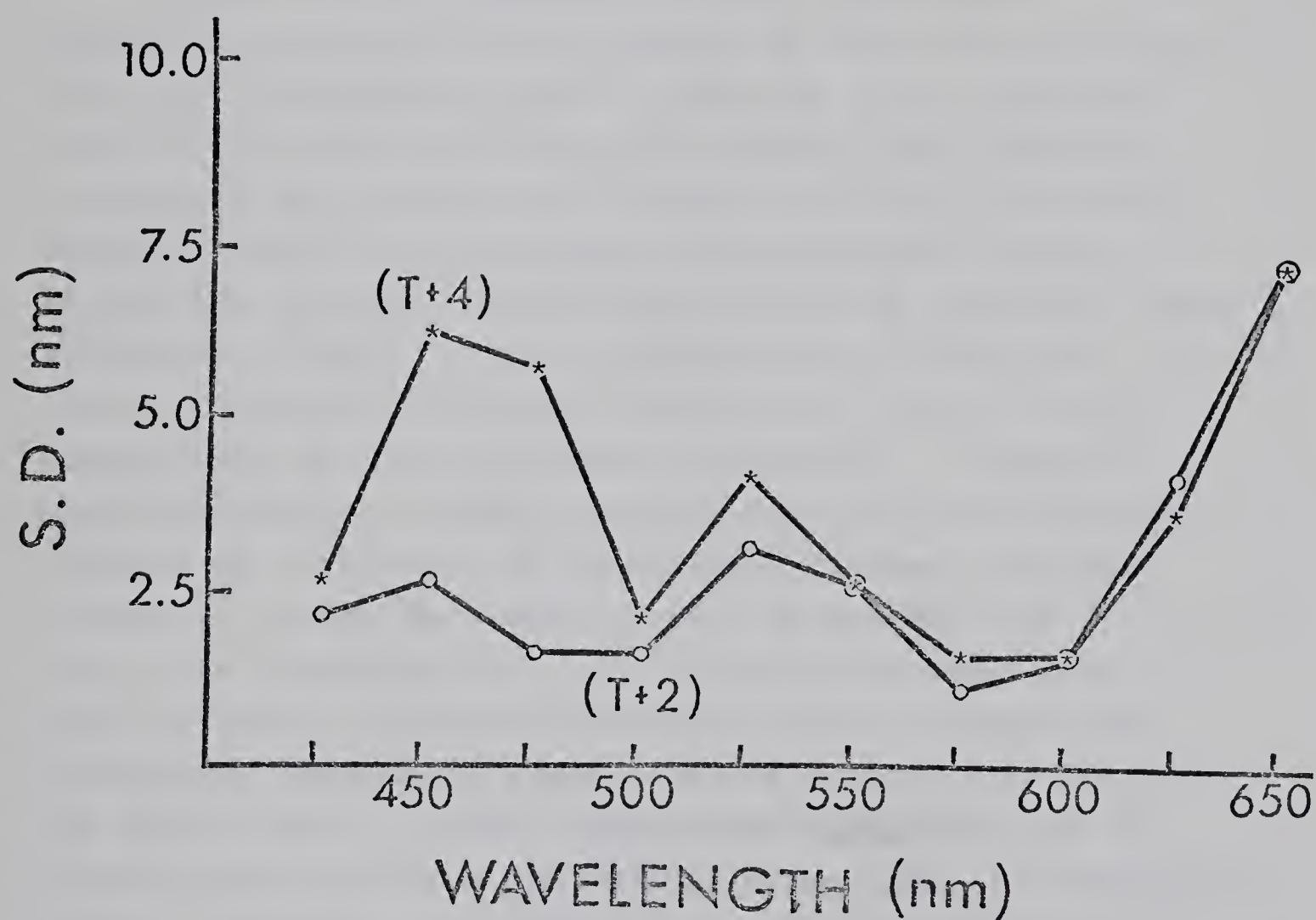


Fig. 2. Pooled average standard deviation of the observers' pulse duration hue matches as a function of stimulus wavelength at threshold plus 2 and 4 log illuminances.

the higher illuminance. Other notable observer variability was restricted to single observer differences: 1) At both illuminances, W.O. reported some positive hue shifts at 500 nm (circa +3.5 nm) while others reported only smaller or negative hue shifts. 2) At the 4 log illuminance, A.H. reported some positive hue shifts at 475 nm (circa +7 nm) while others reported negative hue shifts; the opposite occurs at 600 nm.

Tables 1 and 2 show that inter- and intra-observer variability were greater at short durations and the high illuminance level. This is to be expected since short pulse durations are simply more difficult to observe and since pulse stimuli at high illuminance undergo greater desaturation and brightness changes along with the hue changes being measured (LeGrand, 1968; Wasserman, 1966). It is interesting to note that the intraobserver observer variability bears a close resemblance to hue difference thresholds. Figure 2 shows the pooled average standard deviation of observer matches as a function of wavelength further averaged across all pulse durations at the threshold plus 2 and 4 log illuminances. It is not surprising that these spectral standard deviation curves resemble hue difference thresholds such as those reported by Wright and Pitt (1934), because difference thresholds can be derived from standard deviations (Woodworth and Scholsberg, 1954). However, the similarity of these standard deviations to hue difference thresholds suggests that the observers were generally successful in matching on the basis of hue alone in spite of brightness and desaturation effects; for Kinney (1965) and Wasserman (1966) have shown that these effects for various pulse durations vary with wavelength in a manner which differs from hue discrimination curves.

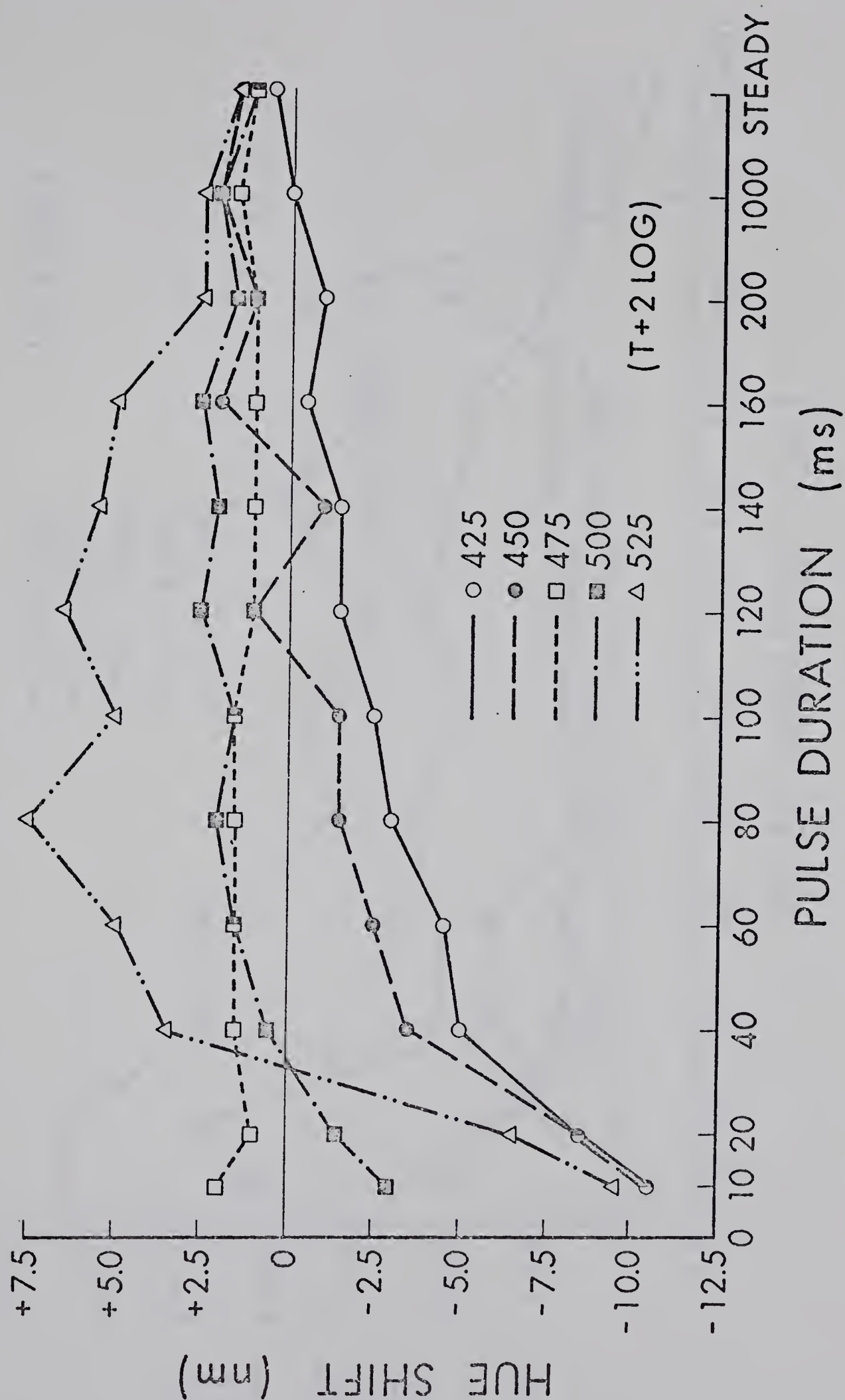


Fig. 3. Hue shift as a function of pulse duration at a threshold plus 2 log illuminance for 425 - 525 nm stimuli.

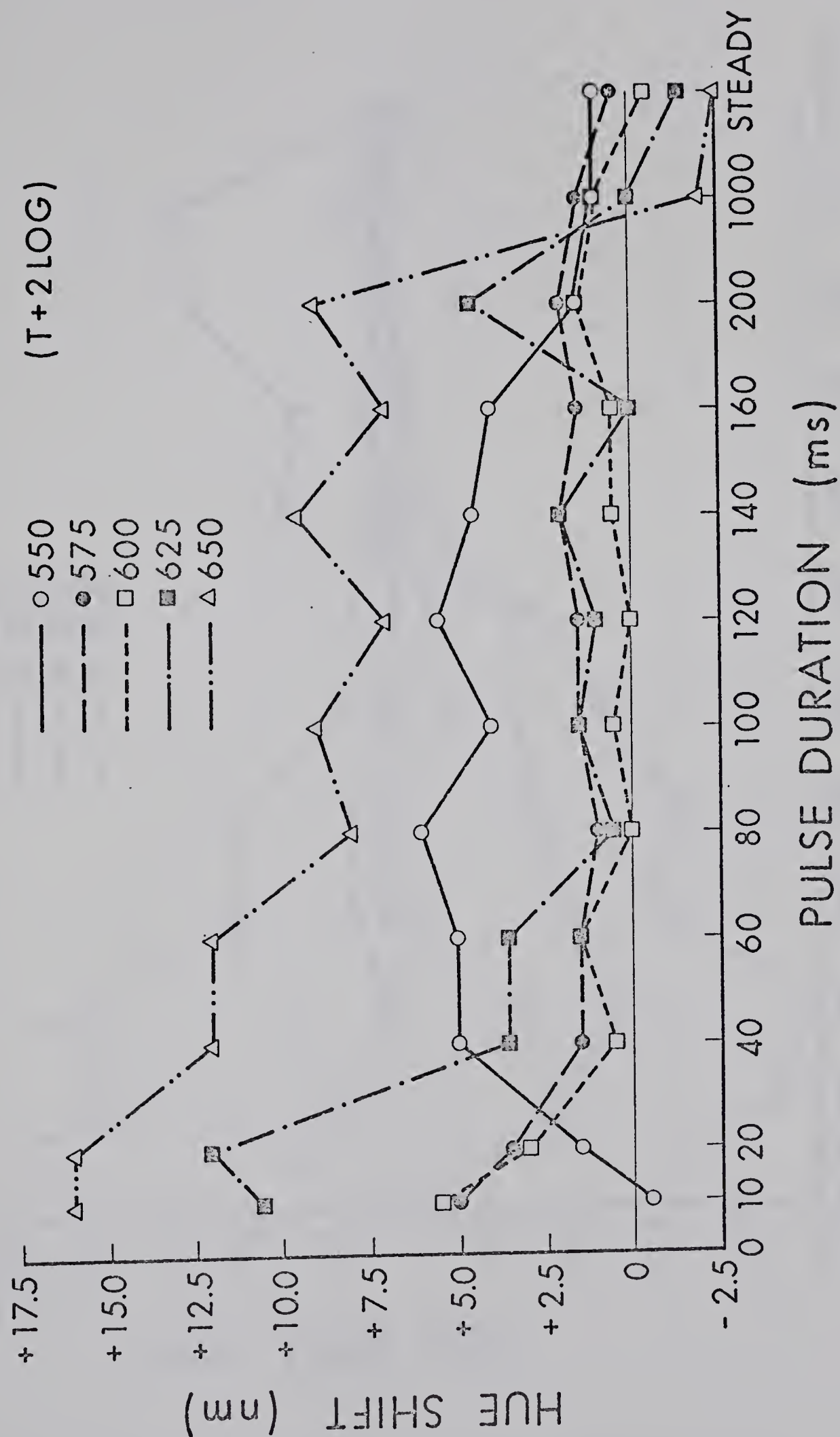


Fig. 4. Hue shift as a function of pulse duration at a threshold plus 2 log illuminance for 550 - 650 nm stimuli.

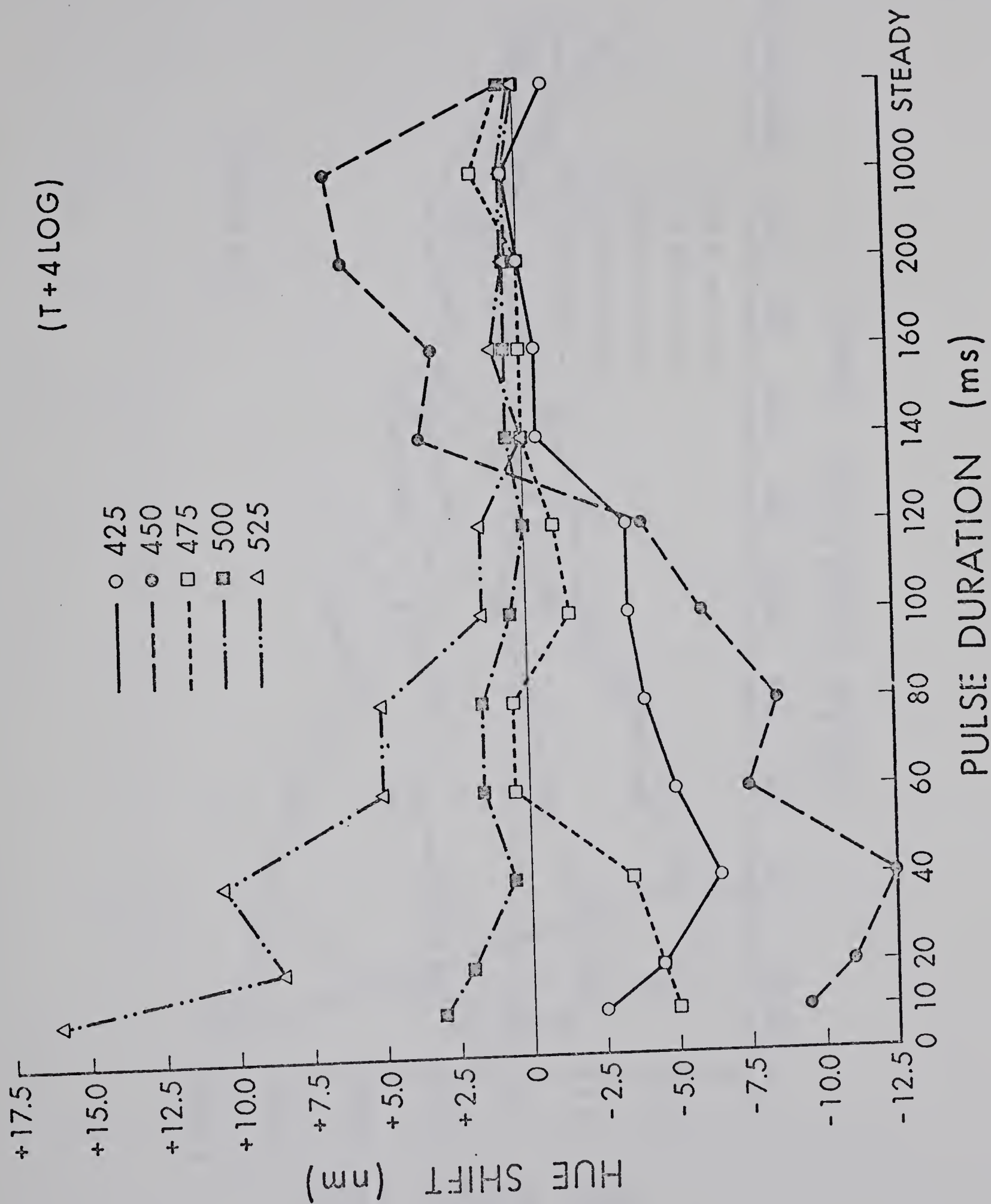


Fig. 5. Hue shift as a function of pulse duration at a threshold plus 4 log illuminance for 425 - 525 nm stimuli.

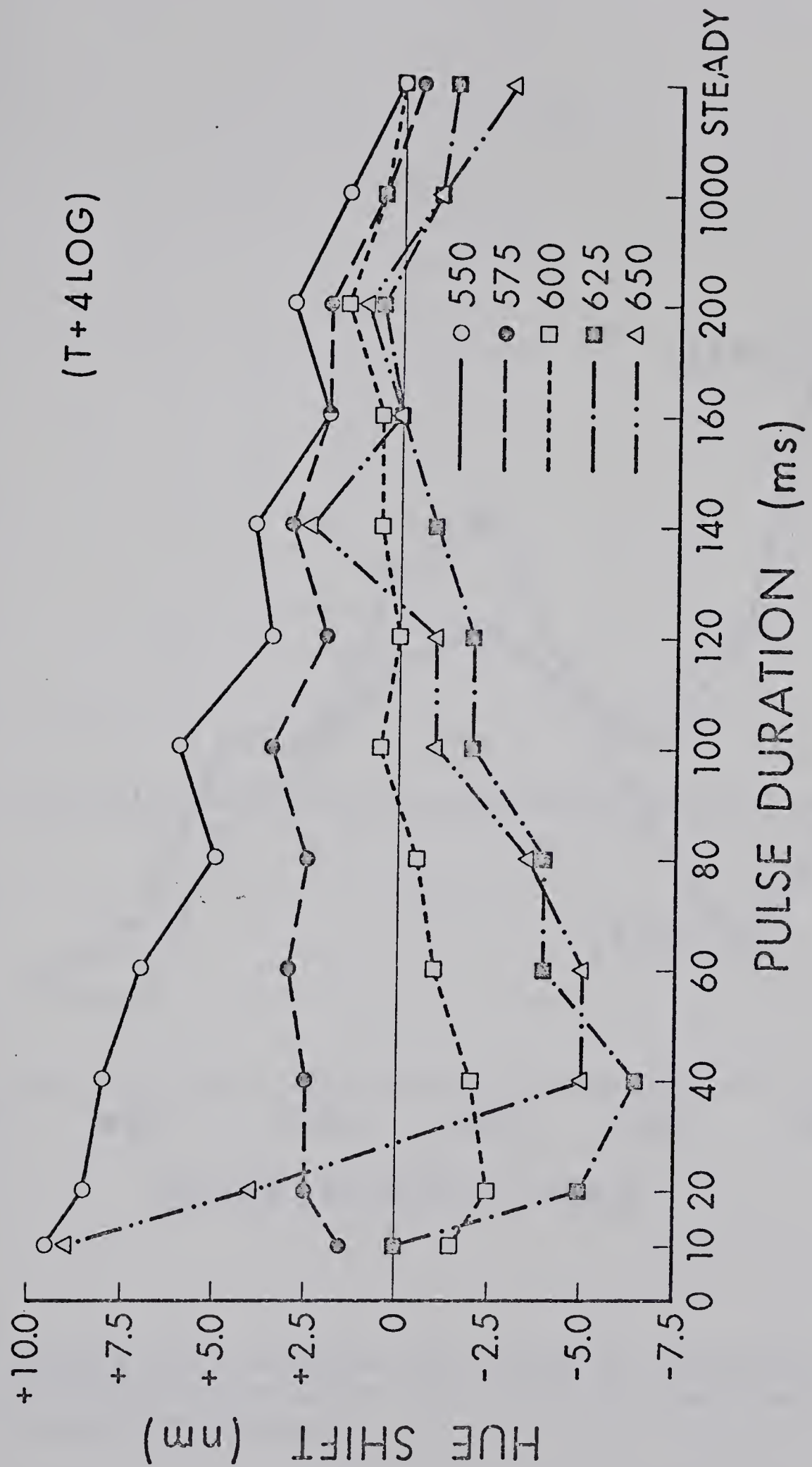


Fig. 6. Hue shift as function of pulse duration at a threshold plus 4 log illuminance for 550 - 650 nm stimuli.

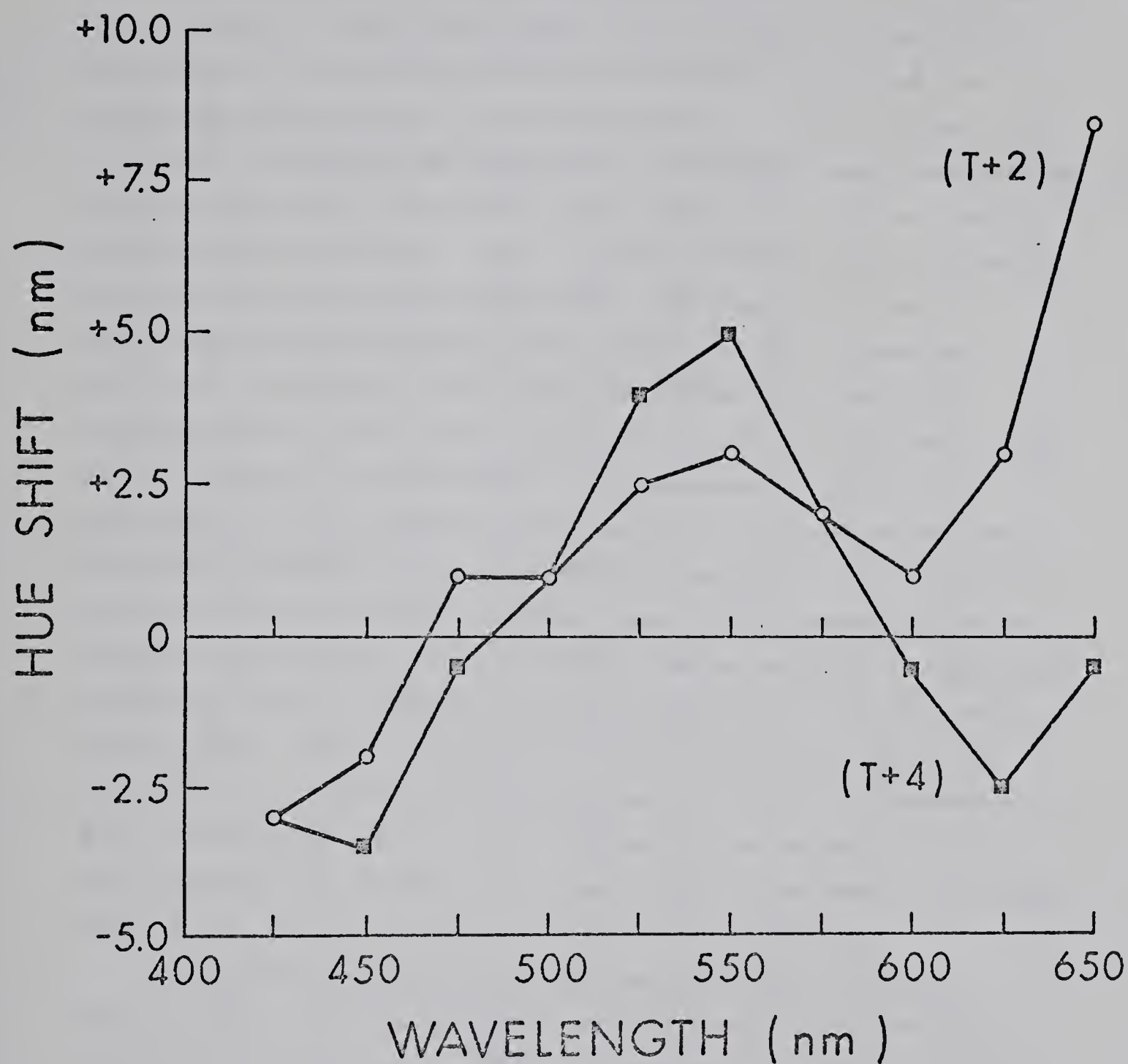


Fig. 7. Average pulse duration hue shifts as a function of stimulus wavelength for threshold plus 2 and 4 log illuminances.

Figures 3-6 show the effect of pulse duration on hue shift at illuminance levels of threshold plus 2 and 4 log illuminances. These figures indicate the following:

- 1) Changes in hue occurred with changes in stimulus duration; the nature of these changes depended on stimulus wavelength and illuminance.
- 2) Stimuli at 475, 500, and 600 nm generally underwent smaller hue shifts than the other stimuli at all durations and at both illuminance levels.
- 3) As pulse duration increased, hue shift magnitudes generally decreased. Two striking exceptions were the large shifts observed with 450 nm stimuli of long duration at the high illuminance level, and the shift by 550 nm stimuli of 80 ms duration at the low illuminance.
- 4) The decrease in hue shift magnitude with pulse duration was more marked at the high illuminance.
- 5) Yet at high illuminance the maximum hue shift occurred at a longer pulse duration with most wavelengths. Stimuli at 550 nm were a notable contradiction.
- 6) At most wavelengths the direction of hue shift did not vary with pulse duration or illuminance level. However, 525 nm stimuli at the low illuminance together with 450 and 650 nm stimuli at the high illuminance indicate that this did not hold for all wavelengths.

Figure 7 shows the average hue shift effect with respect to wavelength as obtained by averaging over all durations. This figure more clearly shows how stimuli at 475 and 500 and at 600 nm underwent little or no change in hue. It also shows the predominant direction of hue shift for the various stimuli which underwent hue changes. At both illuminances stimuli at 425 and 450 nm shifted towards hues normally produced by shorter wavelengths, while stimuli at 525, 550, and 575 shifted towards longer wavelengths. It should be remembered, however, that at some durations

Table 3. Hue shifts in nm produced by various pulse rates of monochromatic stimuli at an illuminance of threshold plus 2 log; average of repeated matches by each observer, and pooled average standard deviation of matches.

PULSE RATE (Hz)	STIMULUS WAVELENGTH (nm)										OBS. & s.d.
	425	450	475	500	525	550	575	600	625	650	
1	-9.7 -12.5 -16.4 -4.4 2.8	-7 -13.3 -13.2 8.9 4.1	0.7 0.8 0.9 2.6 3.4	-3.8 -7.2 -9.1 -1.2 2.3	-8.9 -15.1 -2.8 -10.1 7	0.8 -9 -4.8 -5.6 4.5	7 4 2.4 4.8 3	7.1 4.3 3.6 4.3 3.2	8.8 3.5 -9.2 -2.5 6.4	5.6 2.5 9.4 -5.7 12.7	C.C. M.E. E.J. L.C. SD
3	-8.4 -9.2 -8.9 -4.2 3.1	-8.6 -9.7 -7.9 -3.1 1.8	-1.2 0.8 0.7 8.1 2.7	-3.7 -6.6 -4.4 0.5 2.2	-8.8 -14.7 -10.7 -6.5 3.2	-1.9 -11.1 -4.9 -4.6 5.3	3 1.4 4.6 3.4 1.6	3.9 3 5 3.9 5.1	2.9 3.6 -5.4 0.2 8.2	-8.7 -3.4 15.4 -2.7 13.4	C.C. M.E. E.J. L.C. SD
5	-9.1 -11.8 -11 -2.1 2.4	-5.9 -9.6 -12 -6.9 3.7	-1 0.7 0.7 3.4 4.9	-3.7 -5.3 -7.6 1.4 1.8	-8.9 -13.6 -18.4 9 4.3	-2.9 -10.9 -10.6 -5.4 3.1	4.3 1.6 0.7 1.5 1.7	3.9 0.4 -0.1 1.5 3.2	5.3 2.9 0.7 -1 9	13.1 -2.5 16.5 -4.5 12.2	C.C. M.E. E.J. L.C. SD
7	-10.2 -11 -8.1 -1 3.3	-6 -9.9 -8 -2.5 3.2	-2.6 -6.8 0 3.6 4.1	-3.2 -8.8 -5.4 0.7 2.1	-11.6 -14.4 -12.9 -8.1 2.4	-7.6 -9.2 -6.8 -7 3.5	2 1.2 2.4 2.8 1.4	3.2 1.6 2.4 5.4 2.9	-0.3 -1.1 2.2 0.8 6.7	-0.9 -1.5 17 2 13.4	C.C. M.E. E.J. L.C. SD
9	-12.2 -10.4 -7.4 -2 3.3	-6.2 -11.7 -9.2 -2.5 2.8	-1.1 -2.9 2 4.8 5	-4.2 -4.7 -5.5 0.5 2.7	-12.9 -11.2 -12.5 -5.2 3.9	-5.6 -7.5 -8.5 -4.9 4.5	2.4 0 0.9 1.1 1.2	2.3 1.2 -0.5 1.8 2	4.7 0.3 5.1 -3.9 9.8	-4.2 -6.6 16 -3.7 13.8	C.C. M.E. E.J. L.C. SD
11	-10.7 -10.9 -8.6 0.1 2.9	-7 -10.9 -9.1 -1.1 2.2	-1 -3.2 0.1 4.8 4.3	-4.2 -5.5 -1 0.1 1.7	-11.1 -13.2 -8.3 -7.2 3.1	-6.3 -8.1 -5.8 -6.4 4.3	1.6 0.1 1.4 2 1.9	0 4.4 2 5.8 2.7	8.2 8.8 4.7 3 8.6	19.2 2.3 15.2 10 8.4	C.C. M.E. E.J. L.C. SD
13	-12.7 -12 -10 -1.4 2.1	-6.7 -12.1 -10.4 -4.4 3.4	0 -1.7 0.8 3.9 4.2	-1.7 -5.2 -3.3 1.3 2.3	-10.3 -11.4 -9.7 -5.4 3.1	-4.7 -7.6 -6.4 -5 4	1.8 1.8 2.8 1.3 2.4	1.1 3.8 1.7 3.8 2.3	4.2 4.7 2.6 1.1 9.7	13.8 2.5 17.7 -2.6 11.8	C.C. M.E. E.J. L.C. SD
15	-8.7 -10.5 -7 -1 2.2	-6.5 -11.8 -9.4 -3 2.2	-3.2 -2 -1.4 1.3 4.3	-3.7 -5.3 -1.9 0.4 1.7	-10.2 -11.9 -8.8 -8 3.1	-6.2 -8.4 -5.7 -5.2 3.6	1 1.2 1.1 0.8 2.7	0.7 3.2 1.8 5.1 2.6	-1.4 -2.8 -0.9 4 5.7	10.6 3.8 16.2 7.3 11.1	C.C. M.E. E.J. L.C. SD
17	-9 -8.4 -7.7 -1 3	-6.7 -8.7 -9.6 -2.4 2.8	0.3 -1 2.3 1.5 4	-3.9 -4.7 -0.4 1.9 1.8	-3.5 -11.1 -6.1 -4.9 4.4	-4.1 -8.5 -2.7 -5.1 3.6	0.3 0.8 2.8 0.8 2	2.2 2.2 2.8 2.8 2.1	3.8 5.1 -1.9 -0.9 9.2	18.3 5.3 19.2 3.1 10.4	C.C. M.E. E.J. L.C. SD
21	-9.8 -6 -4.2 -0.5 1.6	-9.5 -6.4 -7.9 -2.1 3.8	-3.3 -5.4 0.8 2.9 2	-3.3 -2.9 -1.6 -1 2.3	-10.1 -7.2 -7.6 -8.7 3.3	-5.7 -5.7 -6.8 -5.2 3.5	-0.7 1.2 0.3 0.3 2	1.3 1.8 2.3 3.8 2.7	6.3 4.3 3 -0.2 5.6	10.1 11.4 14.3 1.9 6.2	C.C. M.E. E.J. L.C. SD
25	-6.1 -6.2 -4.6 -2.2 2.3	-8.8 -3.7 -6.3 -2.1 2	-4.1 -4.1 -1.5 0.9 2.8	-2.8 -3 -1.6 -1.2 1.7	-10.2 -5.6 -6.1 -6.4 2.6	-6.1 -3 -5.1 -4.9 3.2	-0.2 0.3 0.7 0.9 2.1	1 1 1.9 4.1 2	1.6 4.8 ^ 2.3 3.8	5.1 7.9 4.8 7.3 7.2	C.C. M.E. E.J. L.C. SD
31	-7.7 -2.7 -3.3 -2 1.8	-5.5 -1.7 -6.9 -3.9 1.7	-2.4 0.3 -1.2 1 1.9	-1.2 -0.3 -0.7 -0.7 1.5	-7 -3.5 -5.7 -6.7 2.3	-4.3 -2.8 -4.3 -4.9 2.1	-1.4 1.3 0.1 0 1.8	1.7 2.9 1.8 2.8 2.3	-0.7 5.1 -0.6 1.1 4.5	-0.9 7.8 5.6 6 8.1	C.C. M.E. E.J. L.C. SD
37	-4.2 -1.9 -3.6 -2.1 2.4	-4.5 -0.4 -5.8 -2.2 1.9	-2.5 -0.3 -1.4 4.3 2.2	-1.6 -1.7 0.6 1 1.4	-5.3 -5.2 -4.8 -5.2 3.3	-3.6 -1.9 -3.3 -3.1 2.4	0.5 0.8 0.5 1.3 1.9	2 1.8 1.3 1.9 2	3 2.3 -0.8 2.6 3.7	4.6 0.8 8.5 3.9 8	C.C. M.E. E.J. L.C. SD
STEADY	0.6 0.8 0.3 1.5 2.2	1.1 2.8 0.5 2.3 2.2	0.5 0.8 0.8 3.4 0.8	0.3 0.6 1.5 1.8 1.2	-0.1 0.1 2.7 1.1 1.9	-0.6 0.1 1.5 0.6 1.2	-0.1 0.2 0.3 0.3 0.5	-0.6 -0.2 1 -0.2 0.9	0.2 -0.1 -1.4 -1.4 2.1	-0.9 -3.9 0.8 -2.6 5.9	C.C. M.E. E.J. L.C. SD

Table 4. Hue shifts in nm produced by various pulse rates of monochromatic stimuli at an illuminance of threshold plus 4 log; average of repeated matches by each observer, and pooled average standard deviation of matches.

PULSE RATE (Hz)	STIMULUS WAVELENGTH (nm)										OBS. & s.d.
	425	450	475	500	525	550	575	600	625	650	
1	1	1	1.8	5.3	15.6	11.3	2.2	2.8	7.3	14.3	C.C.
	1	0.1	-0.4	0.9	9.3	8.6	-1.1	-6.3	-8.9	-3.6	M.E.
	2.3	-1.1	-1.1	3.2	7.2	1	-0.1	-1.1	1.4	17.6	E.J.
	2.5	0.9	3.3	7.4	17.6	11	0.4	-8.4	-12.7	8	L.C.
	4.2	7.8	2.7	4.9	8.4	5.2	1.2	2.2	5.7	7.2	SD
3	-1.9	6.3	1.4	1.4	14.8	10.6	1.8	-0.1	0.2	9.1	C.C.
	-0.1	-0.7	-2.4	-0.6	4.8	8.1	-0.2	-4.2	-8	-4.3	M.E.
	-0.9	-4.4	-3.9	1.5	13.2	6.4	-0.8	-3.4	-9.6	-8.3	E.J.
	7.9	6.9	2.9	1.6	14.1	8.9	0	-7.4	-13.7	-6.7	L.C.
	3.8	7.8	2.9	3	7.2	2.6	1.5	1.8	3.7	7	SD
5	1.4	2.7	-0.1	-0.4	12.8	7.6	-0.5	-1.2	-3.8	-2.4	C.C.
	-1.1	0	-0.6	0.7	0.7	5.5	-0.5	-6.9	-10.6	-7.7	M.E.
	-2.6	-5.2	-1.8	4.8	16.7	6.3	-0.5	-3.8	-9.1	-7.3	E.J.
	-2.2	-6.9	3.6	4.9	18.6	10.5	-0.1	-5.7	-6.1	-3.5	L.C.
	3.2	6.5	5.3	3.4	7.8	3.4	1.9	2.9	9.2	10.3	SD
7	-0.5	0.7	1.5	1.8	6.8	6.4	-2.2	-4.5	-7.6	0.5	C.C.
	0.1	2.6	-2.2	0.8	13.4	5.5	-0.8	-8	-13.9	-13.4	M.E.
	-0.9	-2.8	1.1	3.3	13.9	5.5	-0.3	-4.1	-12.8	-5.1	E.J.
	3.5	2.9	6.4	4.4	19.3	8.6	0.3	9.7	0.1	2	L.C.
	4.3	8.7	3.4	3.3	5.1	3.2	1.4	2.1	7.7	9	SD
9	1.9	2.3	2.5	0.9	10.8	5	-1.7	-5.5	-10	-11.1	C.C.
	-1.3	-1.2	-0.9	0.3	10.8	8.4	-1.7	-8.2	-15.2	-12	M.E.
	-3.6	-4.5	-0.6	-0.7	12.7	7.3	-0.1	-2.2	-9.3	7.1	E.J.
	-1.4	-3.7	1.2	4.5	19.8	10.9	0.1	1	5.5	0	L.C.
	1.7	4.9	3.3	2.4	6.7	2.3	1.1	6.5	9.6	11.3	SD
11	-2.2	-2.8	-0.5	1.3	6.8	5.1	-4.2	-6.7	-10.9	-7.2	C.C.
	-1.2	-2.2	-3.2	2.3	12	7.7	-2.7	-8.5	-14.3	-12.8	M.E.
	-0.5	-2.1	-1.3	1.9	13.1	5.7	-2.9	-8.1	-14.2	-0.4	E.J.
	-1.7	1.3	1.6	4.3	15.9	8.4	-1.4	-11.7	-13.7	-8.2	L.C.
	2.4	5.8	3.7	3	6	2.6	1	2.6	3	12.6	SD
13	2.7	-4.5	1	-0.4	6.6	2.3	-2.4	-6.4	-10.6	-7.7	C.C.
	-1.9	-1.6	-2.1	0.4	9	6.9	-3.6	-9	-13.5	-5.7	M.E.
	0.1	-4.7	0.5	1.8	11.7	6.3	-2	-3.4	-8.3	12.4	E.J.
	1.1	1.3	1.6	13.6	19.4	4.4	-0.5	-5.4	3.5	3.1	L.C.
	3.1	5.4	4.2	3.5	6.5	4.5	2.6	5.8	8.4	9.4	SD
15	0.2	-3.7	2.3	-1	5.3	3.3	-3.3	-6.2	-11.7	-10.7	C.C.
	-1.2	-3.9	-4.9	2.3	11.6	3.3	-3.7	-9	-11.6	-5.2	M.E.
	-1.9	-3.9	-0.5	1.4	12.7	4.2	-4	-7	-12.2	3.5	E.J.
	-0.5	-6.7	-1.4	12.8	9.8	5.3	-1.7	-9.7	-14	0	L.C.
	2.6	3.8	2.8	4.8	6.1	4.6	1.7	2.4	5.1	7.4	SD
17	-0.5	-7.5	-0.5	-1	3.8	-0.5	-5.2	-6.6	-7.7	-0.8	C.C.
	-0.3	-3.8	-6.3	2.2	8.6	4.6	-3.7	-8.9	-9.9	-6.4	M.E.
	-0.8	-6.9	-2.9	0.9	8.3	2.5	-2.2	-4.7	-6.9	13	E.J.
	0.3	-8.7	-6.4	4.5	19	6.8	-0.7	-7	-1.9	3.5	L.C.
	1.6	3.7	4.7	4.4	5.2	3.2	1.1	1.9	6.2	9.5	SD
21	0.3	-4	-1	1.9	4.9	2.6	-3.6	-6.9	-8	-1.3	C.C.
	-1.1	-1.1	-0.9	0.4	10.3	3.9	-3.1	-6.8	-9.3	-4.2	M.E.
	-0.5	-4.3	-3.5	2.5	10.5	3.6	-4.8	-7.5	-4.8	4.7	E.J.
	-0.2	-8.5	-4.5	5.8	14.9	7.3	-1.5	-8.5	-2.4	9.9	L.C.
	1.5	3.6	3.7	4.2	4.3	2.2	1.1	2.4	4.7	7.7	SD
25	1.5	4.6	0.1	-0.4	2.6	0.5	-3.1	-6.2	-9	-6.2	C.C.
	0.7	-0.7	-0.8	1.9	8.3	4.7	-1	-3.9	-7.6	-1.2	M.E.
	0.3	-4.6	-1.4	2.8	7.3	3.8	-3	-4.9	-5.4	5	E.J.
	0.3	-6	-2.9	5.5	12.8	6.8	-2.4	-5.4	-0.7	6.5	L.C.
	1.4	2.8	3.6	1.8	3.6	2.2	1	2	3.7	7.2	SD
31	2.7	3	-0.1	0.3	-0.2	-1	-2.3	-3.1	-4	-4.2	C.C.
	0	1.3	-1.3	0.4	2.1	1.3	-2.2	-2.3	-3	-0.8	M.E.
	0.6	-2.7	-0.3	1.5	4.3	1	-2.2	-2.7	-3.3	6.9	E.J.
	1.6	-2.9	0.1	3.8	7.4	0.4	-1.9	-5.7	-2.1	9.3	L.C.
	1.2	3.7	2.2	1.2	2.8	3	0.6	1.5	2.5	4.8	SD
37	3.2	5.8	-2.4	0.3	0.2	-0.7	-1.8	-0.7	-1.7	0.6	C.C.
	0.7	-2.4	-0.2	1.3	2.7	-1.8	-1.4	-0.9	2.7	1.9	M.E.
	0	-3.6	-0.4	0.5	1	-1.3	-1.9	-1.1	0.6	9.2	E.J.
	0.5	-2.2	1.8	2.4	1.9	0	-2	-4	2.3	7.4	L.C.
	1.3	3.3	2.5	0.9	1.6	3.9	1	1.1	2.7	4.6	SD
STEADY	1.4	2.9	1.2	0.6	-0.7	-0.9	-0.8	-0.2	-2.1	-5.1	C.C.
	1.3	1.6	2.4	1.3	0	-0.8	-0.3	0	-1.2	-9.1	M.E.
	0.9	-1.3	0.8	0.4	-0.7	-0.8	-0.1	-0.3	-1.5	-6	E.J.
	0.1	-1.7	0.8	2	-0.2	-0.5	-0.6	3	-4.7	-0.5	L.C.
	1.5	-2.7	3.3	0.6	1	1	0.9	0.6	2.3	2.5	SD

525 nm stimuli shifted towards shorter wavelengths at the low illuminance and 425 nm stimuli shifted towards longer wavelengths at the high illuminance. Stimuli at 625 and 650 nm mainly shifted towards longer wavelengths at the low illuminance and towards shorter wavelengths at the high illuminance. But as pointed out earlier, the variability of these red hue shifts should be kept in mind.

PULSE RATE

The effects of pulse rate on hue at illuminance levels of threshold plus 2 and 4 log units are shown in Tables 3 and 4. Again edge effects and desaturation probably contributed to large observer variability as to direction and magnitude of hue shifts at 625 and 650 nm. There was also some notable observer variability with 450 and 475 nm stimuli at the high illuminance. These stimuli were difficult to match at low rates due to desaturation, an effect also noted by Bartley and Nelson (1960) and Horst and Muis (1969). Other notable observer variability is restricted to a single observer: 1) At the low illuminance, L.C. reported positive hue shifts (circa +5 nm) of 475 nm stimuli while others reported negative hue shifts. 2) At the high illuminance, L.C. reported that some 475 and 500 nm stimuli underwent larger positive hue shifts (circa +5 and +10 nm) than other observers reported.

Tables 3 and 4 show that inter- and intraobserver variability was greater at lower rates and the high illuminance. This is to be expected since low pulse rates are simply more difficult to observe and since intermittent stimuli undergo greater brightness and saturation changes at high illuminance (Ball, 1964). It is

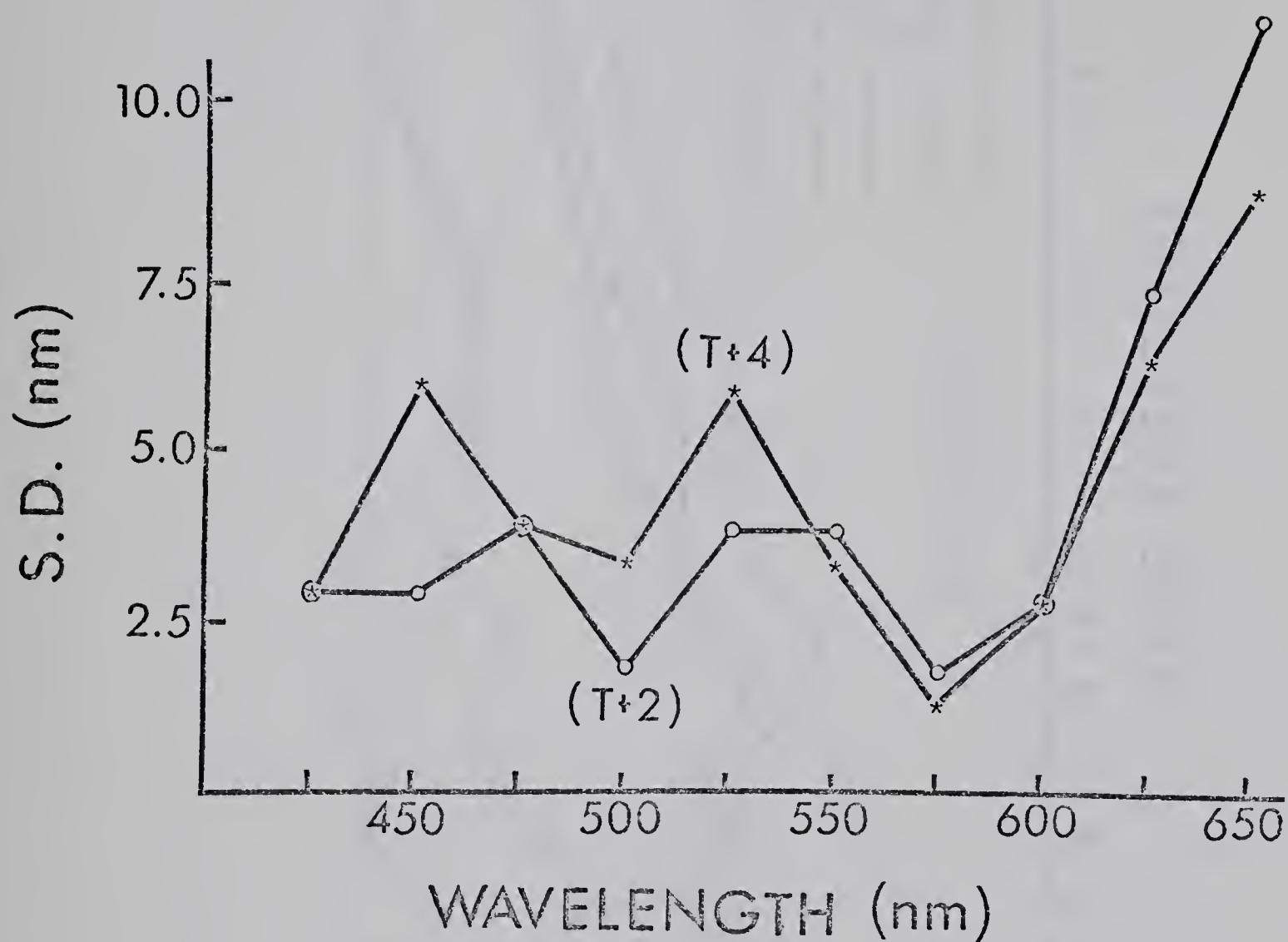


Fig. 8. Pooled average standard deviation of the observers' pulse rate hue matches as a function of stimulus wavelength at threshold plus 2 and 4 log illuminances.

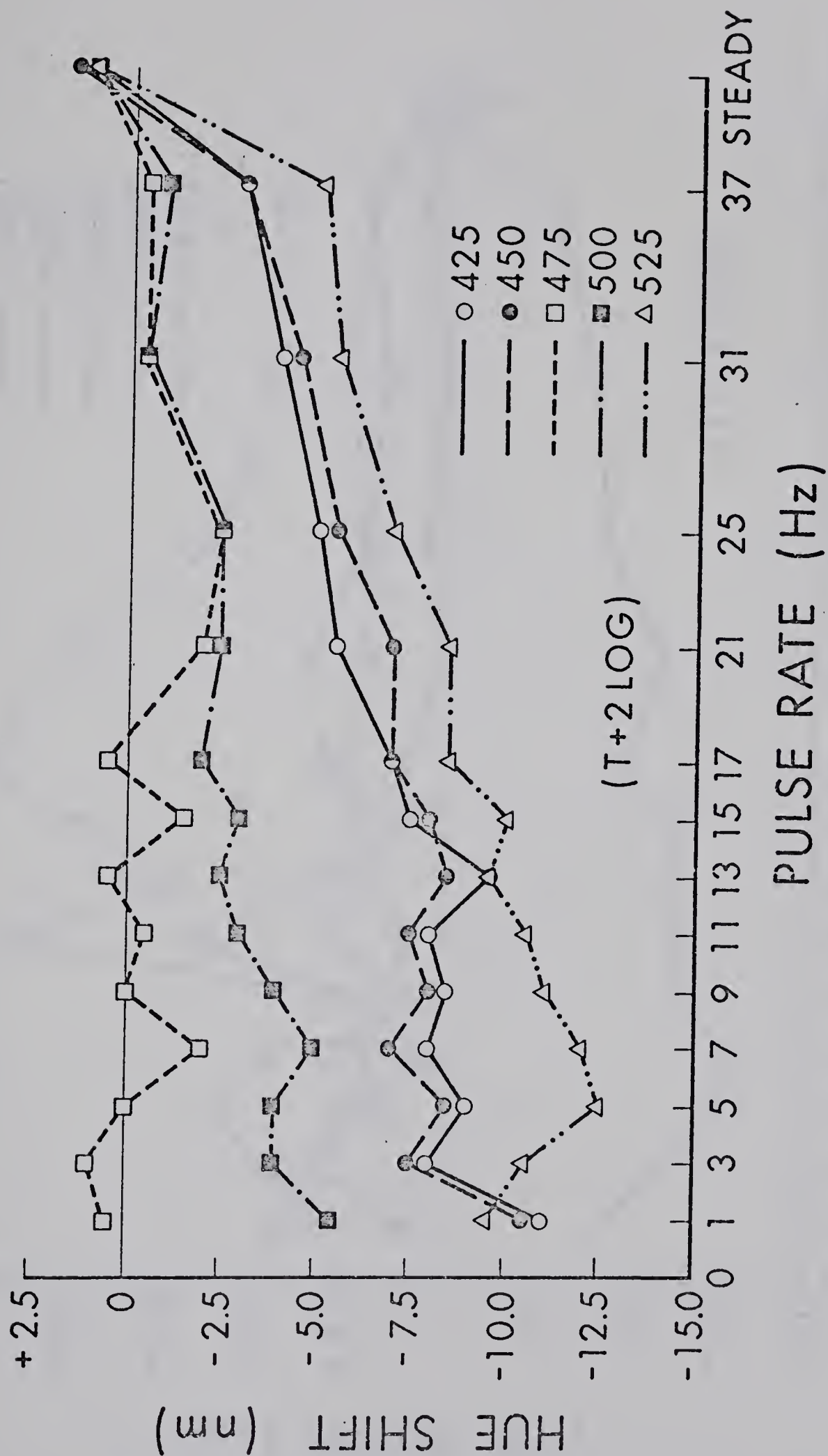


Fig. 9. Hue shift as a function of pulse rate at a threshold plus 2 log illuminance for 425 - 525 nm stimuli.

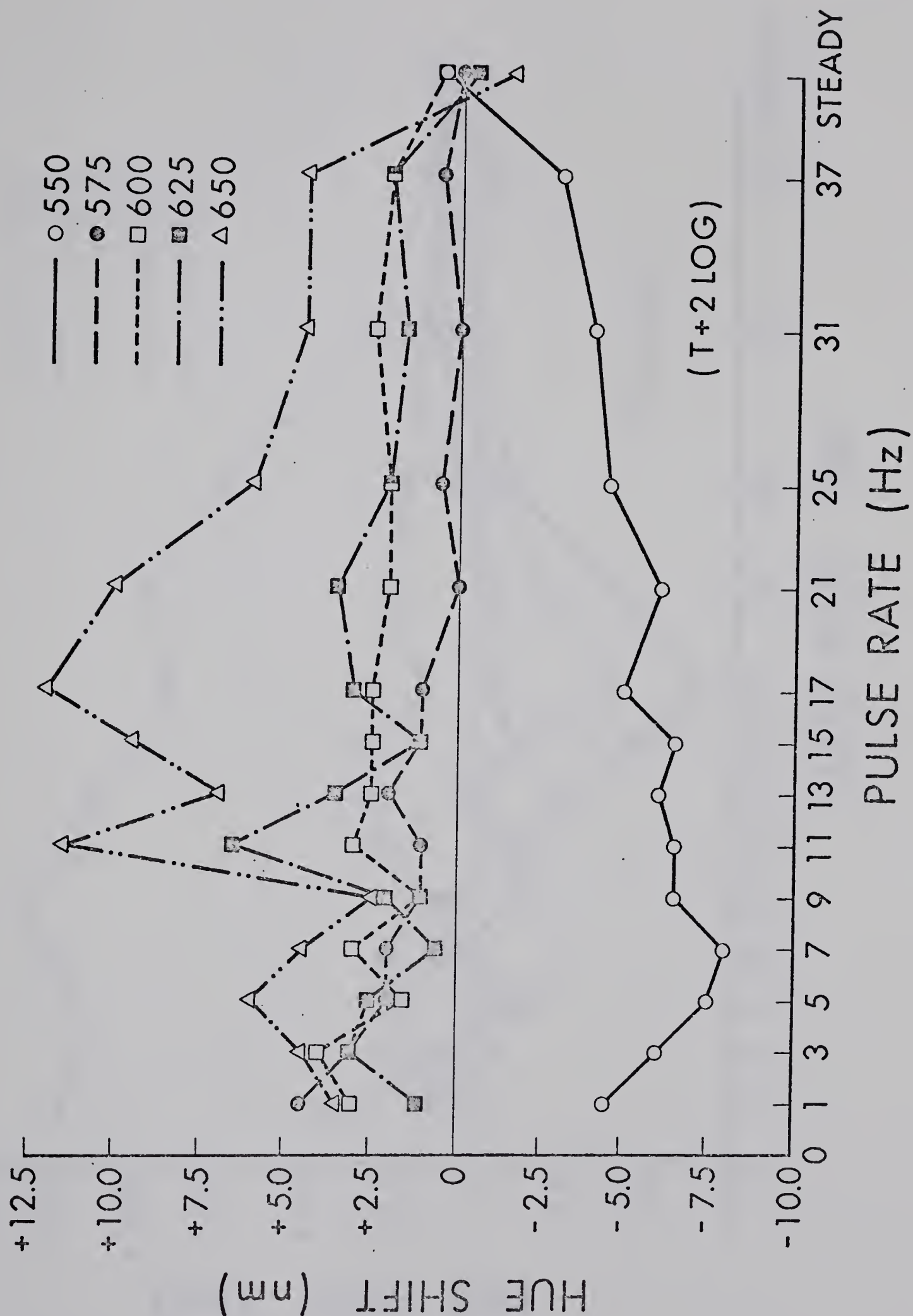


Fig.10. Hue shift as a function of pulse rate at a threshold plus 2 log illuminance for 550 - 650 nm stimuli.

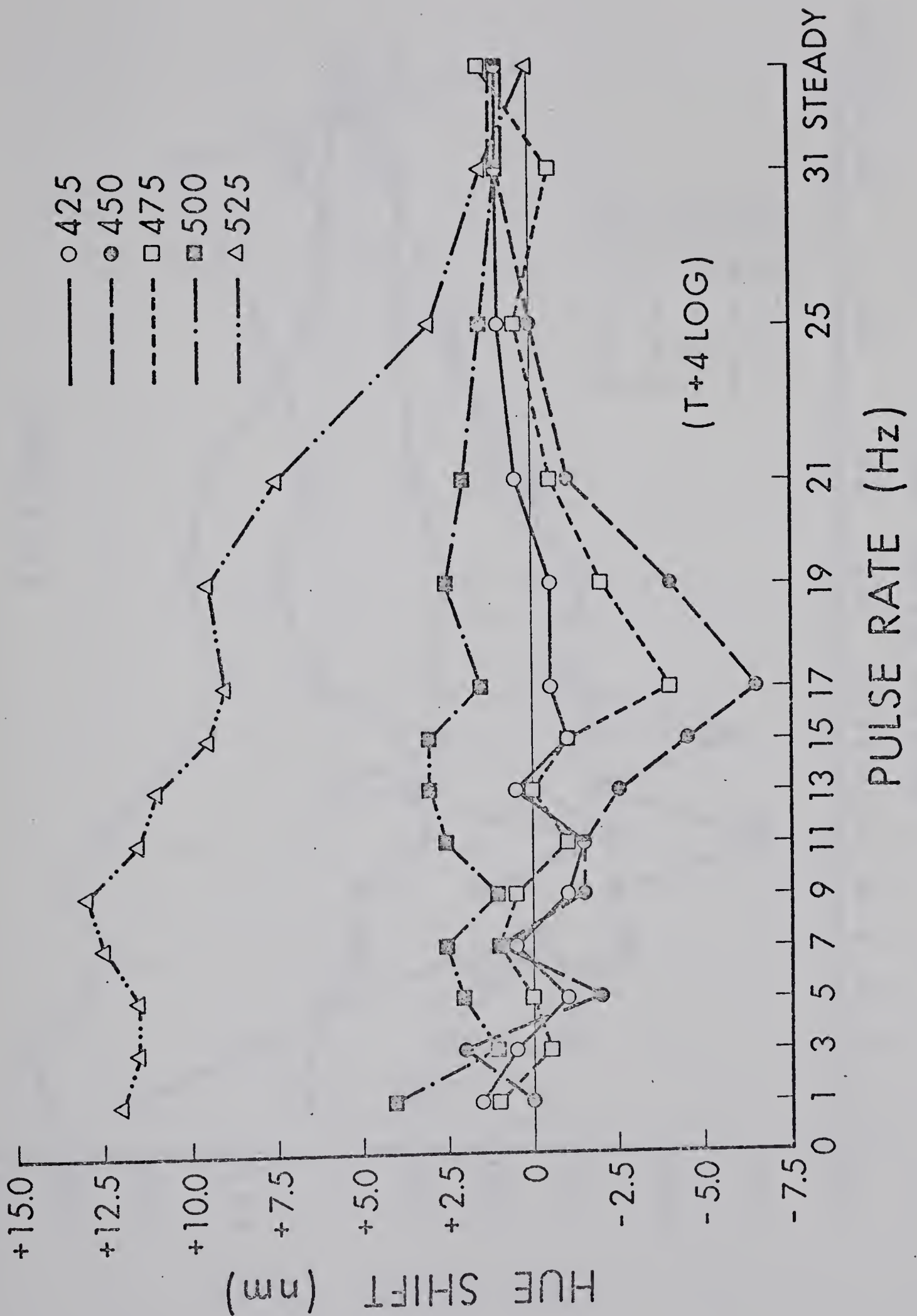


Fig. 11. Hue shift as a function of pulse rate at a threshold plus 4 log illuminance for 425 - 525 nm stimuli.

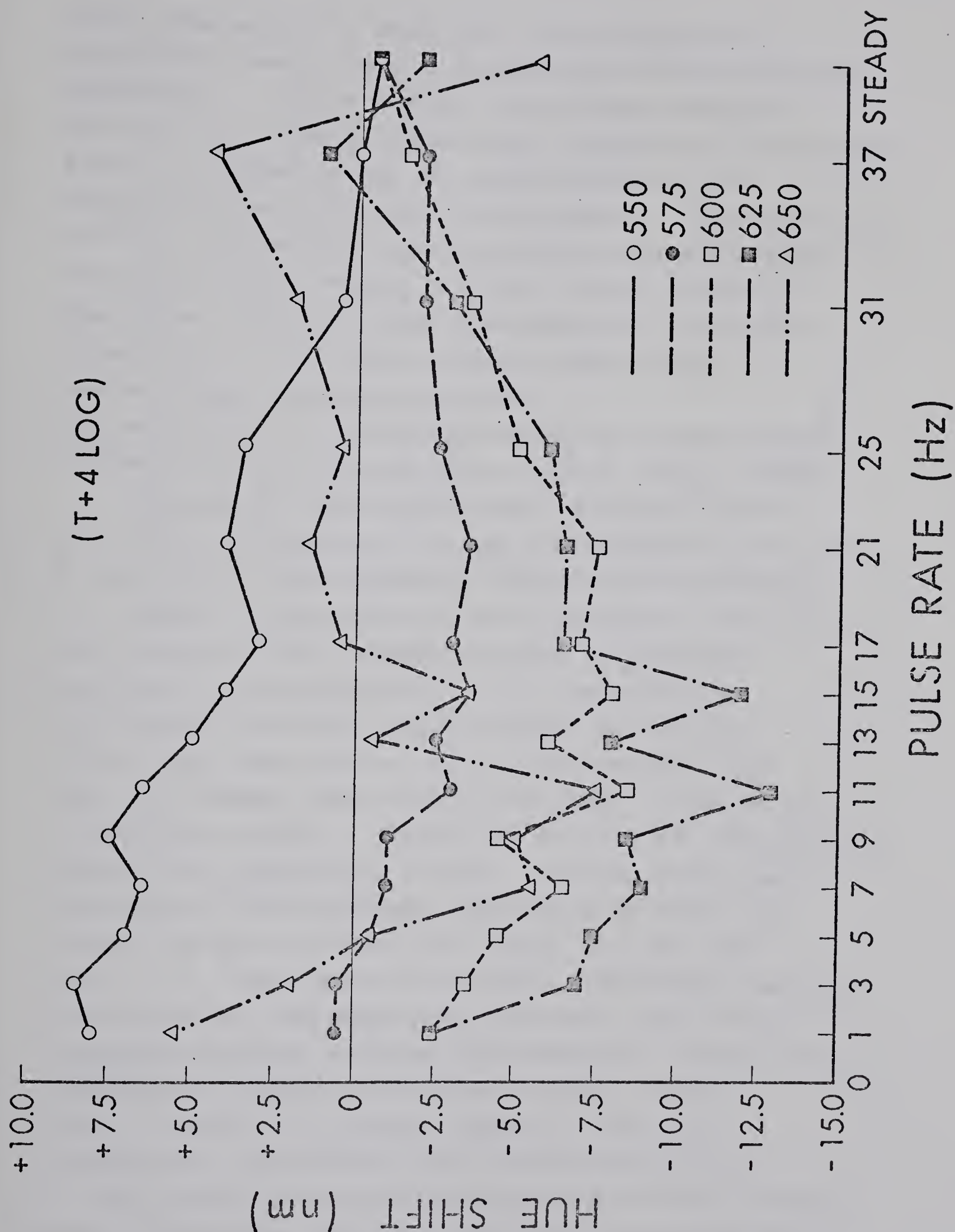


Fig. 12. Hue shift as a function of pulse rate at a threshold plus 4 log illuminance for 550 - 650 nm stimuli.

again interesting to note that the interobserver variability bears a close resemblance to hue difference thresholds. Figure 8 shows the average standard deviation of observer matches as a function of wavelength further averaged across all pulse rates at the threshold plus 2 and 4 log illuminances. The similarity of these standard deviation curves to hue difference threshold curves (Wright and Pitt, 1934) suggests that these observers were also generally successful in matching on the basis of hue alone because intermittency produced brightness and saturation vary with wavelength in a manner which differs from hue discrimination curves, (Ball, 1964).

Figures 9-12 show the effect of pulse rate on hue shift at illuminance levels of threshold plus 2 and 4 log units. These figures indicate the following:

- 1) Changes in hue occurred with changes in pulse rate; the nature of these changes depends on stimulus wavelength and illuminance.
- 2) Some stimulus wavelengths underwent larger changes in hue than others, but there seems to be no wavelength which does not undergo some notable hue shift at one of the illuminance levels. Stimuli at 475 and 575 nm generally shifted less than other stimuli, but one should not overlook all hue shifts of these stimuli since the j.n.d. for hue at these wavelengths is less than 2 nm.
- 3) There appears to be no relationship between pulse rate and the magnitude of the hue shift which is general to most stimulus wavelengths. Pulse rates above 21 Hz seem to produce smaller hue shifts but the behavior of 650 nm stimuli at the high illuminance contradicts even that generalization.
- 4) The pulse rate producing maximal hue shift differed with illuminance level for most stimulus wavelengths.

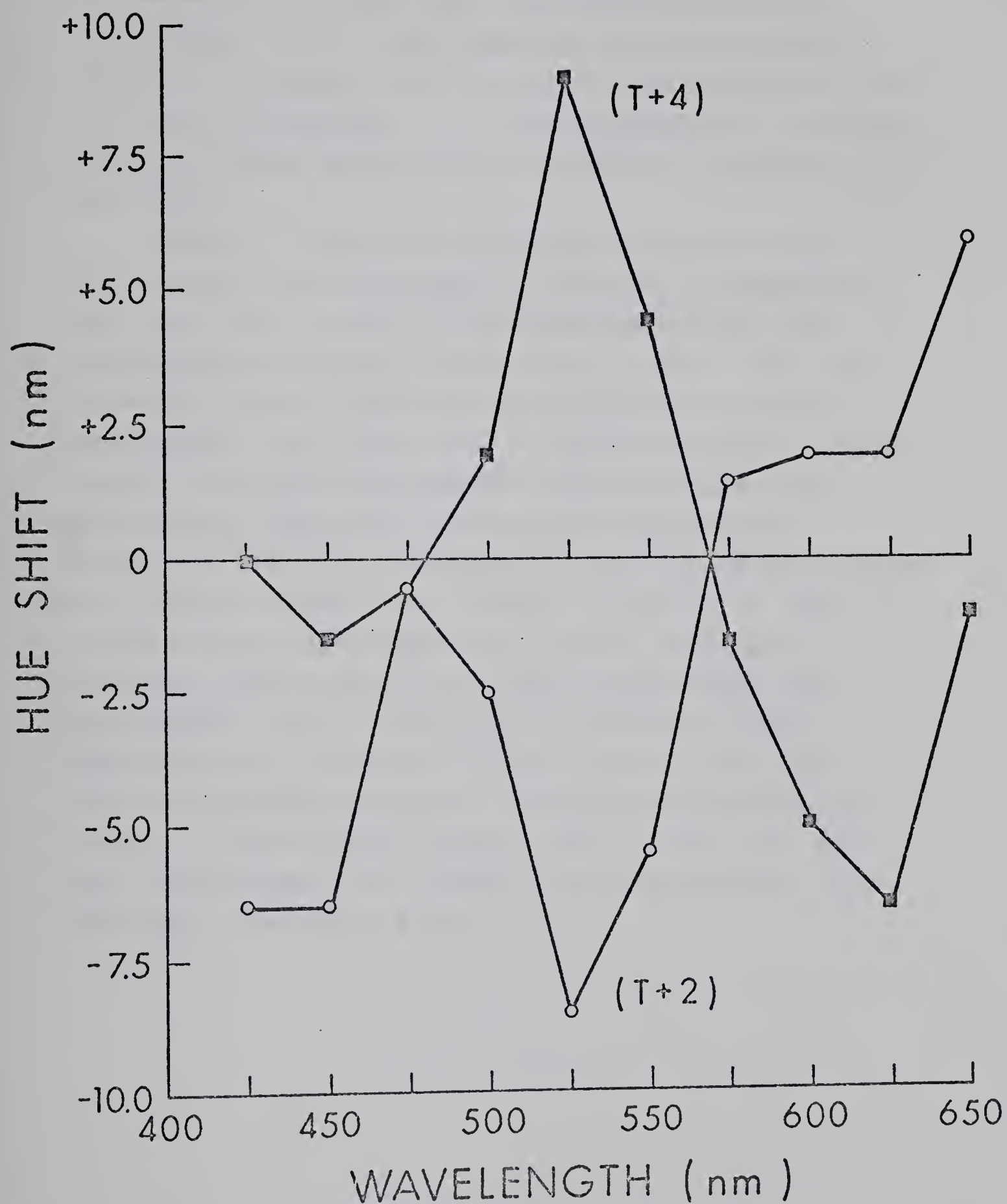


Fig. 13. Average pulse rate hue shifts as a function of stimulus wavelength for threshold plus 2 and 4 log illuminances.

5) There was almost no significant change in direction of hue shift as pulse rate was varied at a given illuminance level. The remarkable exception was the 650 nm stimulus which changed direction twice at the high illuminance. 6) As illuminance is changed, all wavelengths above 475 nm changed in direction of hue shift.

Figure 13 shows the average hue shift effect with respect to wavelength as obtained by averaging over all pulse rates. The figure manifests the difference of the two illuminance levels. At the threshold plus 2 log illuminance, pulsed stimuli at wavelengths from 575 to 650 nm were matched to steady stimuli of longer wavelength, while at the 4 log illuminance they were predominantly matched to stimuli of shorter wavelength. The opposite occurred to a greater extent with stimuli from 500 to 550 nm. At the 2 log illuminance 425 and 450 nm stimuli underwent substantial hue shifts towards shorter wavelengths, but at the higher illuminance this effect was much reduced. This figure indicates that 475 and 575 nm stimuli changed only minimally in hue. However, one should bear in mind the fact that these stimuli did undergo some appreciable hue shift at a few pulse rates.

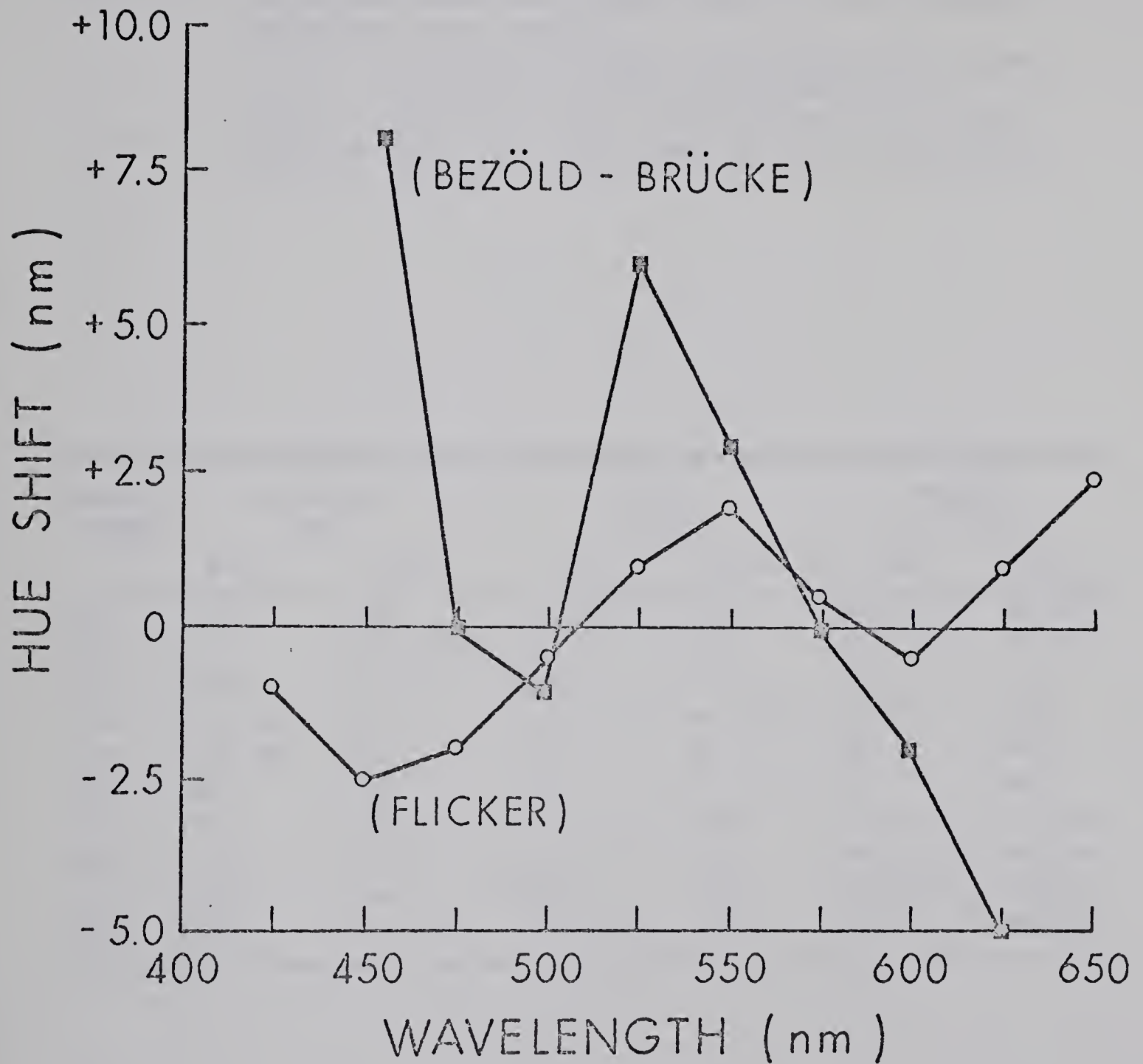


Fig. 14. Comparison of Bezöld - Brücke and average flicker hue shift effects as functions of stimulus wavelength.

Table 5. Pulse parameters producing maximal hue shifts as pulse duration, pulse rate, and flicker frequency are varied.
 (+ or - alongside number indicates the direction of the hue shift. Two entries in a column indicates that two maxima in the hue shift effect are undergone by the wavelength of that row.)

Wave-length (nm)	Duration (ms)		Rate (Hz)		Flicker (T+5 log)	
	T+2	T+4	T+2	T+4	Hz	ms
425	-10	-40	-1 15-	-11	-10 5-	-25 40-
450	-10	-40 1000+	-1	-17	-15 5-	-17 40-
475	-10	-20	-25	-17	-14	-18
500	-10 160+	+10	-1 7-	+1 13+	+7 3-	+36
525	-10 80+	+10	-5	+9	+8	+83
550	+80	+10	-7	+3 9+	+7	+36
575	+10	+100	+1	-15	-15 7+	-17 36+
600	+10	-2.5	+3 11+	-11	-9 13+	-28 18+
625	+20	-40	+11	-11	+13 11-	+18 23-
650	+15	+10 50-	+17 11+	-11 1+	+13 9-	+18 28-

DISCUSSION

The original purpose of measuring the hue shifts of pulse stimuli as their duration and rate are varied separately was to attempt to determine what parameter of flicker stimulation was responsible for the temporally induced flicker hue shifts. The main effect of wavelength flicker hue shifts from Nilsson and Nelson (1971) is presented in Fig. 14 for comparison with duration and rate hue shifts in Figs. 7 and 13. Surprisingly it is the duration hue shifts which are most similar to the flicker hue shifts. At the threshold plus 2 log illuminance, duration and flicker hue shifts are in the same direction at all wavelengths except for the small shifts at 500 and 600 nm, and it is the duration hue shifts which shift maximally at 550 nm as do flicker hue shifts. However, a comparison in Table 5 of durations and intermittency rates producing maximal hue shifts in the present study with data of Nilsson and Nelson (1971) reveals that flicker hue shifts are most similar to the 4 log pulse rate condition in terms of temporal parameters producing shifts. These considerations suggest that flicker hue shifts represent a combination of pulse duration and rate effects, though a look over Table 5 indicates the combination is by no means simple.

The results clearly reveal that changes in hue occur with change in the duration or rate of monochromatic light pulses. The occurrence of pulse duration and pulse rate hue shifts does not necessarily depend on conditions which produce brightness enhancement of these stimuli. As illuminance is decreased both Broca-Sulzer and Brücke-Bartley brightness enhancement effects decrease in magnitude (Horst and Muis, 1969;

LeGrand, 1968); the present study shows that neither pulse duration or pulse rate hue shifts are particularly smaller at the lower illuminance. Wavelengths around 500 and 580 nm undergo maximal Broca-Sulzer and Brücke-Bartley brightness enhancement (Ball, 1964; Wasserman, 1966); these are wavelengths which undergo minimal hue shift as either pulse duration or pulse rate is varied. The temporal conditions which produce maximal Broca-Sulzer and Brücke-Bartley brightness enhancement are 100 ms and 10 Hz respectively and do not vary with stimulus wavelength (Horst and Muis, 1969; Wasserman, 1966). The present study shows that the temporal condition producing maximal pulse duration or pulse rate hue shifts varies with stimulus wavelength. Table 5 shows that maximal pulse duration hue shifts generally occur at durations much shorter than 100 ms and about half of the pulse rate hue shifts occur at frequencies very different from 10 Hz.

The effect of illuminance on the temporal parameter producing maximal hue shift reveals some additional facts about the relationship between temporal hue shifts and brightness enhancement effects. As illuminance is decreased Broca-Sulzer and Brücke-Bartley brightness enhancement effects occur maximally at longer durations and lower frequencies. In the present study pulse duration hue shifts show a reverse trend by shifting maximally at shorter durations at the lower illuminance; pulse rate shifts show no directional trend in rates producing maximal hue shift as illuminance is decreased. However, Table 5 shows that the pulse parameters producing maximal hue shift are closer to the pulse parameters producing maximal brightness enhancement at the higher illuminance. These trends show that

temporal hue shifts differ more at low than at high illuminance from brightness enhancement effects.

Depending on conditions pulse duration and pulse rate hue shifts both resemble and differ from Bezöld-Brücke illuminance hue shifts which might be expected to accompany and Broca-Sulzer or Brücke-Bartley brightness changes by these stimuli. Compare the Bezöld-Brücke hue shifts in Fig. 14 with the pulse duration hue shifts in Fig. 7 and with the pulse rate hue shifts in Fig. 13. (The Bezöld-Brücke hue shift data were obtained from Wildt and Bouman, 1968, for that stimulus condition, Fig. 3, $B_2 = 1.7$, which showed hue shifts of the most comparable magnitude to those of the present study.) All three hue shift phenomena are minimal at 475 and 575 nm. At the higher illuminance both duration and rate hue shift effects bear a further resemblance to Bezöld-Brücke hue shifts in that the direction of hue shift is the same for wavelengths longer than 475 nm; at high illuminance all hue shifts are towards longer wavelengths for stimuli between 500 and 575 nm and towards shorter wavelengths for stimuli beyond 575 nm. Pulse duration and pulse rate hue shifts differ from the Bezöld-Brücke effect at both illuminance levels when stimulus wavelength is shorter than 475 nm. But it is at the low illuminance that the temporal hue shifts differ most markedly from Bezöld-Brücke hue shifts. At low illuminance, pulse rate hue shifts are opposite in direction to Bezöld-Brücke hue shifts at all wavelengths; pulse duration hue shifts are also opposite except for stimuli between 500 and 575 nm. While the predominant trend of 500 and 575 nm duration hue shifts at low illuminance is similar to Bezöld-Brücke hue shifts, Fig. 1 shows that 525 nm stimuli of low illuminance do shift towards shorter

wavelengths at short durations.

Both pulse duration and pulse rate hue shift effects at low illuminance occur at conditions not dependent on brightness enhancement and are very different from Bezöld-Brücke hue shifts. This lends support to conclusions reached in earlier flicker studies (Fry, 1945; Horst and Muis, 1969; Nilsson and Nelson, 1971) that temporally induced color changes represent unique phenomena arising from an interaction of temporal parameters of stimulation and temporal response characteristics of color pathways. The present study shows that temporal hue shifts are different at high and low illuminances. The magnitude of this difference suggests that temporal hue shifts are dichotomous phenomena encompassing at high illuminance an effect similar to Bezöld-Brücke hue shifts and at low illuminance an effect which is contrary to Bezöld-Brücke hue shifts.

AN EXPLANATION OF TEMPORAL HUE SHIFTS

The discovery that temporal hue shifts are similar to Bezöld-Brücke hue shifts at high illuminance but contrary to them at low illuminance suggests a simple way to conceptualize temporal hue shift phenomena. This explanation recognizes that the three types of cone receptors overlap considerably in spectral response characteristics (Brown and Wald, 1964; Marks, Dobelle and MacNichol, 1964) and that these spectral response characteristics are further transformed during transmission by color-opponent neural pathways (DeValois, Smith, Kitai, and Karoly, 1958). But spectral sensitivity is not the only factor which determines the amount of activity produced in the neural pathways from a receptor.

Receptors and their color-opponent neural pathways also have temporal response characteristics which alter the resultant activity depending on the timing of the stimulus. The effects of very low frequency stimulus timing are the well known adaptation phenomena. The effects at higher frequencies are less understood but include phenomena such as masking and enhancement (Bartley, 1968). It is proposed that temporal hue shifts can be understood if we consider how spectral and temporal response characteristics of receptor pathways are likely to interact at various illuminance levels.

At high illuminances, stimuli at a given wavelength are able to excite not only the type of receptor maximally sensitive to that wavelength but also, to a lesser extent, the other receptor types. Thus as illuminance is increased, wavelengths below 475 nm begin to excite green receptors in addition to blue receptors. Also at higher illuminances wavelengths between 500 and 575 nm begin to excite blue receptors in addition to green receptors, but, due to the greater spectral overlap of green and red receptors, these wavelengths will excite red receptors more than blue receptors. Similarly wavelengths above 600 nm begin to excite green receptors in addition to red receptors.

As higher illuminances elicit responses from additional receptor types, the resultant total activity no longer resembles that produced by the original wavelengths. Rather, the result resembles activity produced by wavelengths intermediate between the original and wavelengths characteristic of the spectral sensitivity of the additional receptor type. This rationale predicts that at high illuminances: 1) The hue produced by wavelengths

below 475 nm shifts towards the hue normally produced by longer wavelengths. 2) The hue of wavelengths between 500 and 575 nm also shifts towards that of longer wavelengths. 3) The hue of above 600 nm shifts towards that of shorter wavelengths. 4) The hue of wavelengths intermediate to the spectral sensitivity of color receptors will undergo minimal hue shift since these hues normally result from the activity of multiple receptor pathways.

This explanation of color effects at high illuminance has been suggested by Hurvich and Jameson (1955) and by Walraven (1961) to account for Bezöld-Brücke hue shifts. It is proposed that it can also be applied to temporal hue shifts at high illuminance. Under these conditions the activity in additional receptor pathways will be further enhanced at certain temporal parameters of stimulation depending on the temporal response characteristics of the various types of receptor pathways. The obtained hue shift curves represent the interaction of these temporal response characteristics with overlapping spectral response characteristics. The description seems in accord with observations in the present study, that wavelengths which don't undergo Bezöld-Brücke hue shifts don't undergo temporal hue shifts, and that desaturation effects were prevalent only at the high illuminance. The description also is in accord with previous data on saturation and brightness changes by spectral stimuli of various pulse durations and flicker frequencies (Ball, 1964; Horst and Muis, 1969; Wasserman, 1966).

At low illuminances, stimuli at a given wavelength are able to excite only the type of receptor maximally sensitive to that wavelength. However, the color-opponent pathways from this

receptor type remain susceptible to further activation as a result of stimulus timing. Any such enhanced activity will not be counterbalanced by activity of the opponent color response since the prerequisite receptors would not be stimulated to begin with. Thus as illuminance is decreased, wavelengths below 475 nm excite only blue receptors and the subsequent B+Y-, Y+B- color-opponent pathways. At certain temporal parameters these wavelengths further activate the B+Y- pathway while inhibiting the R+G- pathway. Similarly stimuli above 600 nm can further activate the R+G- pathways while inhibiting the G+R- pathways. (The effect of stimuli around 575 nm on the Y+B- and B+Y- pathways is not immediately evident since temporal activation of this pathway would be confounded with effects in the G+R- and R+G- pathways; there being no Y receptor.)

As the temporal parameter of stimulation enhances activity in receptor pathways, and as lower levels of illumination restrict this activation to a given color response of that pathway, the resultant total activity will no longer resemble that normally produced by the original wavelengths. Rather, the result resembles activity produced by wavelengths which are more distant from wavelengths characteristic of the spectral sensitivity of the opponent color response of the given pathway. In accord with present observations, this rationale predicts that at certain temporal parameters of low illuminance stimulation: 1) The hue produced by wavelengths below 475 nm shifts towards the hue normally produced by shorter wavelengths. 2) The hue of wavelengths between 500 and 575 nm shifts towards the hue of shorter wavelengths. 3) The hue of wavelengths above 600 nm shifts towards that of longer wavelengths.

4) The hue of wavelengths around 500 and 575 nm which are intermediate to the spectral sensitivity of the component spectral sensitivities of color-opponent pathways will undergo minimal hue shifts since temporal effects will be counterbalanced by occurring in both color component responses.

The essential features of this explanation of color effects at low illuminance draw upon ideas proposed by Hurvich and Jameson (1955) and Walraven and Bouman (1966). What has been added is simply a consideration of the effects of temporally induced enhancement of neural activity on the response of color-opponent pathways. The obtained hue shift curves represent the consequences when this enhancement is restricted to a single type of receptor pathway by low illuminance. Since these low illuminance effects are restricted to a given type of pathway, it is proposed that these hue shift curves directly reflect the temporal response characteristics of specific color pathways. These hue shift curves reveal that the temporal parameter of stimulation which produces maximal hue shift varies with wavelength. Similar conclusions that color pathways have unique temporal response characteristics have been proposed repeatedly in previous studies dealing with diverse problems of color (Fry, 1945; Ikeda and Boynton, 1962; Ingvar, 1959; Nelson, 1971; Shipley, Jones and Fry, 1968; Talbot, 1951; Troland, 1933).

While the above two explanations describe probable effects at extreme luminance levels, it also seems reasonable to expect that at intermediate illuminance levels a combination of these effects will prevail. Such a view might explain the rather dramatic changes in direction of hue shift which occurred with some wavelengths as either pulse

duration or rate was varied in the present study. Also this explanation has considered only the probable effects of temporal enhancement on color processes; there is evidence that temporally induced inhibitory effects occur at both neural and sensory levels under certain conditions of stimulus timing (Donchin and Lindsley, 1965; Schiller (1968). The foregoing explanation predicts that conditions which produce inhibitory masking effects would at low illuminance result in hue shifts contrary to those described above, while such hue shifts at high illuminance would be confounded with a Bezöld-Brücke type effect.

Investigation of such masking color effects together with the present data may lead to explanations of color induction phenomena such as Benham's top and Festinger, Allyn, and White's (1971) results. Finally the proposed explanation of low illuminance temporal hue shifts suggests that these hue changes result from temporally altering the activity within a given type of color pathway. Further research along this line may reveal the extent to which temporal response characteristics are utilized to convey hue information within, as opposed to between, neural pathways as color is integrated with other perceptual responses at the cortical level.

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APPENDIX A

Cortical Potentials Evoked by
Spectral Stimuli of Various Durations:
An Attempt to Break the Code for Hue.

The finding in the present study that hue can be altered by altering the duration of a spectral stimulus indicates that hue of an isolated stimulus is to some extent a wavelength independent and temporally dependent response of the visual system. Previous studies of visually evoked cortical potentials by Shipley, et al. (1968) and Ciganek and Ingvar (1969) have found evidence of a temporal coding of wavelength information. The finding of conditions under which hue is independent of wavelength suggests that it might be possible to determine if perceived hue as well as stimulus wavelength is temporally coded in visually evoked cortical potentials. Therefore the cortical potentials evoked by spectral stimuli were recorded for stimulus conditions similar to those for which hue shifts were measured as a function of stimulus duration. Records of these potentials were then analyzed in an attempt to find characteristics related to hue as well as wavelength.

METHOD

Bipolar scalp EEG was recorded from locations similar to those used by Shipley, et al. (1968) along the anterior-posterior cephalic midline 2 and 4 inches above the inion using zinc electrodes recommended by Montagu and Coles (1966) with a sweat isotonic (Robinson and Robinson, 1954) paste of zinc sulfate electrolyte in an inert cornstarch base recommended by Edelberg and Burch (1962). A

ground electrode was attached to the ear lobe. Electrode impedances were within the 20 to 50 K ohms range. A Motorola MC 1456 operational amplifier was secured to the subjects head to act as a 1000X preamplifier. The EEG signal was further amplified 1000X by a Techtronix 122 amplifier to approximately 2 volts for oscilloscope monitoring and recording on a Hewlett-Packard model 3960-B instrumentation tape recorder along with pulse signals of stimulus duration and verbal commentary. Averaged evoked potentials were monitored using a Technical Measurement Corporation CAT 400C.

The EEG was recorded from two observers showing normal color vision on the Ishihara test. Stimuli of 10 to 1000 ms duration at 425 to 650 nm were presented at threshold plus 2 and 4 log illuminances. These stimuli were similar in configuration to those for which hue shifts were measured and were produced by the same apparatus. Alternate durations and illuminances were presented on a given day and counterbalanced as to order across days. Wavelengths presented at each duration were alternately in ascending or descending order counterbalanced across days. Twenty presentations were made of each stimulus condition for a given day and replicated three times across days to yield a total of 60 responses to each stimulus. In order to standardize the effects of duration at a given wavelength across observations, stimulus duration presentations were alternated at 2 sec intervals with 1000 ms duration presentations of the same wavelength. This use of a standard stimulus was suggested by Uttal (1965), but it subsequently proved to be impractical to analyze the data accordingly due to equipment limitations.

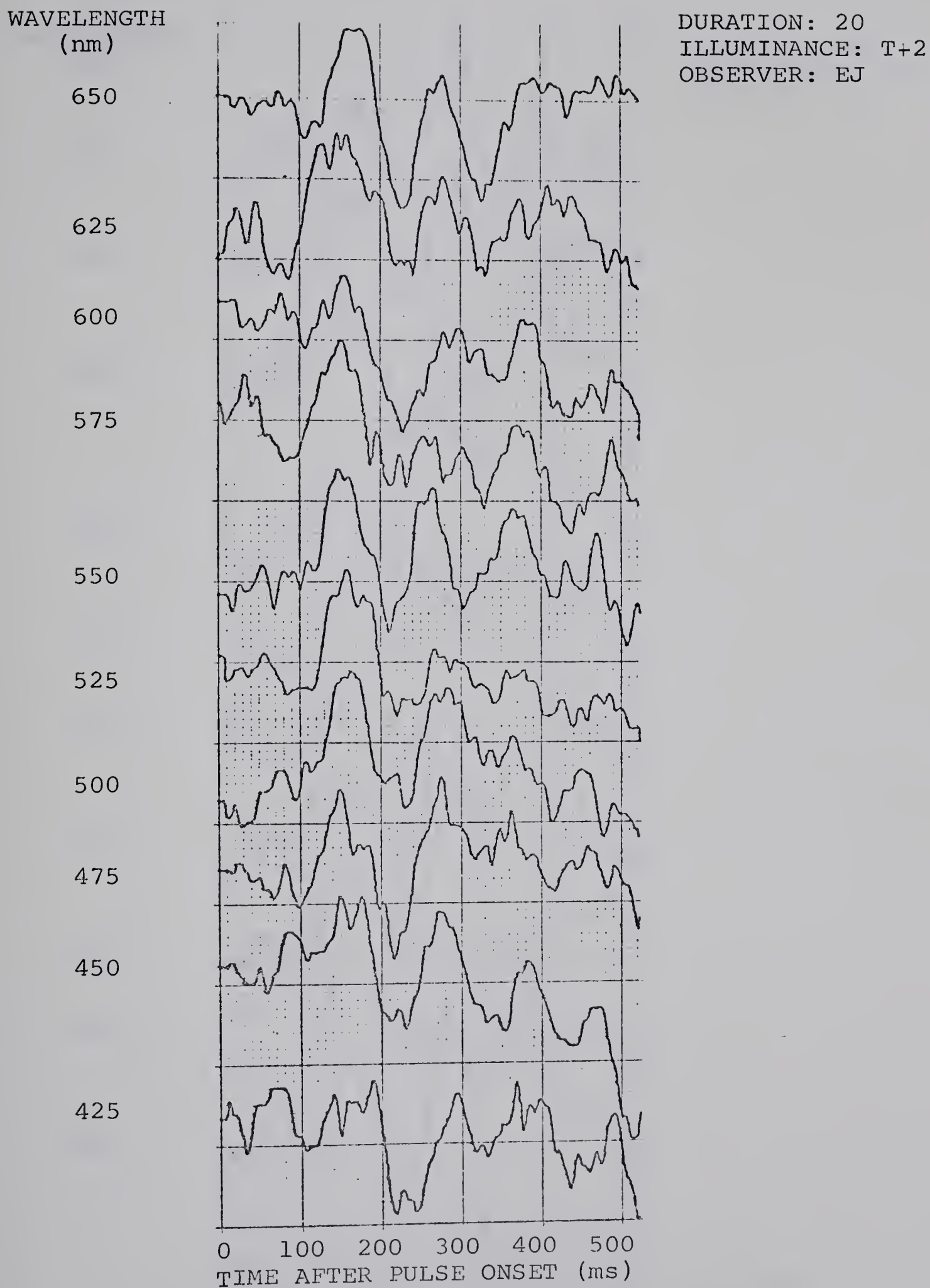


Fig. 1. Averaged cortical potentials evoked by a 20 ms stimulus of various wavelengths.

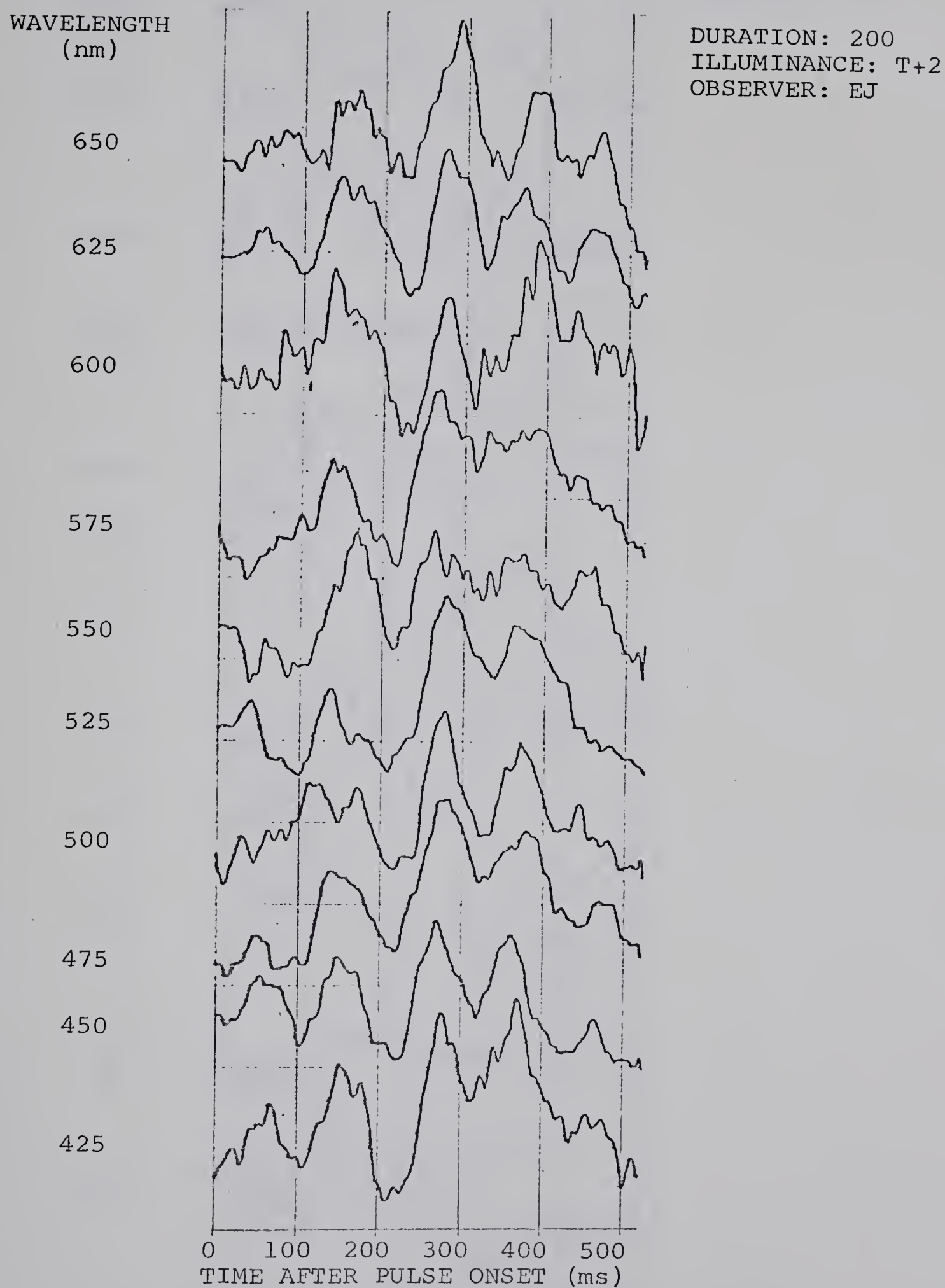


Fig. 2. Averaged cortical potentials evoked by 200 ms stimuli of various wavelengths.

PULSE
DURATION
(ms)

WAVELENGTH: 650
ILLUMINANCE: T+4
OBSERVER: TN

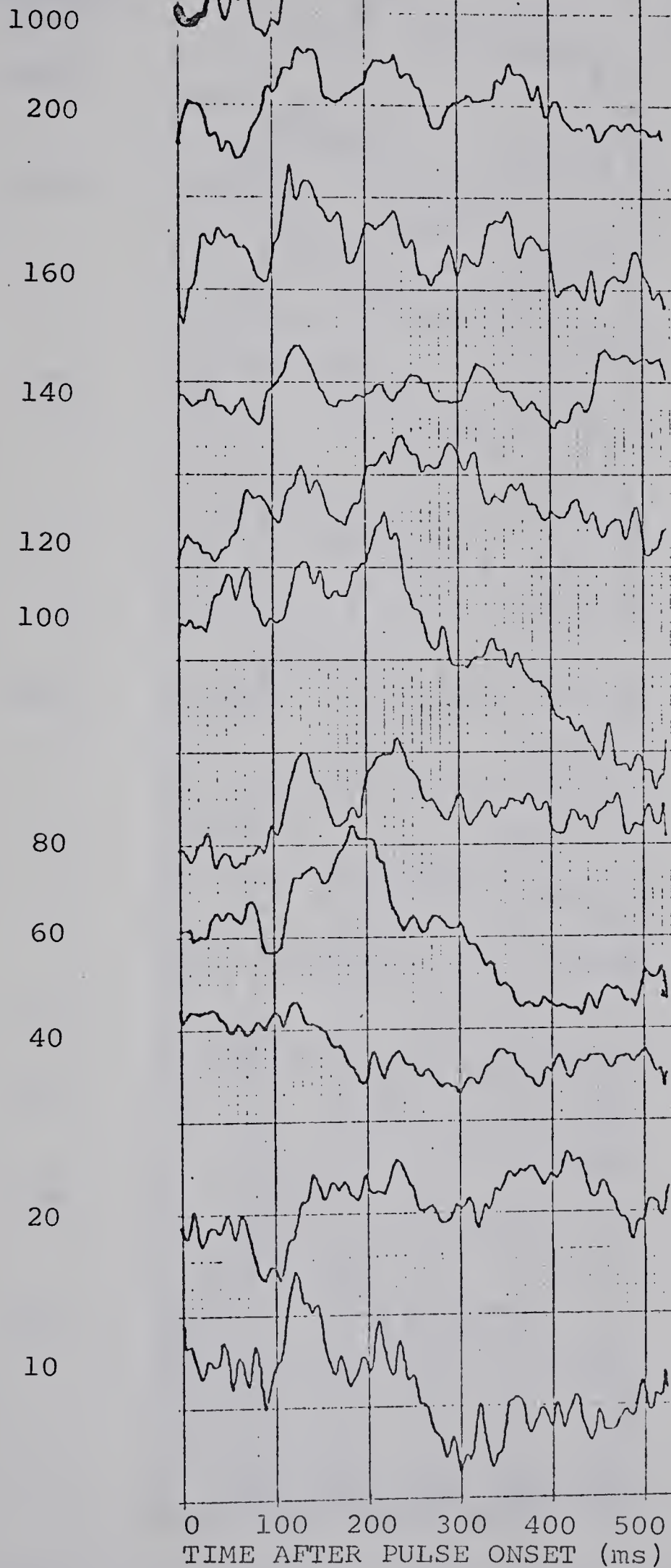


Fig. 3. Averaged cortical potentials evoked by various durations of a 650 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 625
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

80

60

40

20

10

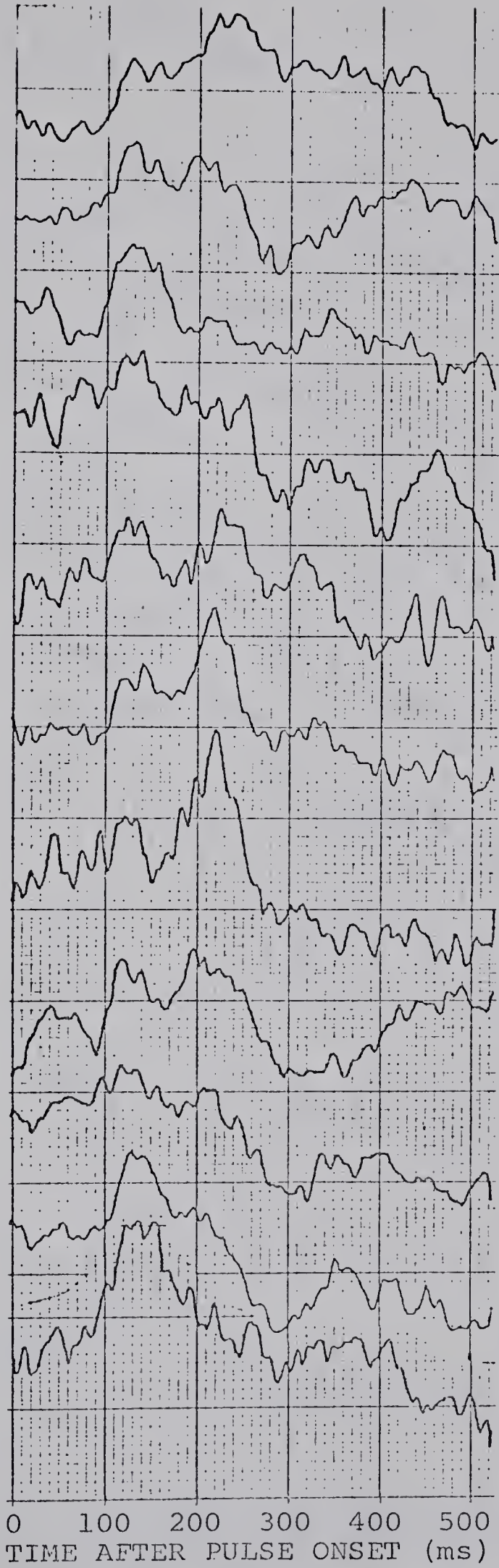


Fig. 4. Averaged cortical potentials evoked by various durations of a 625 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 600
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

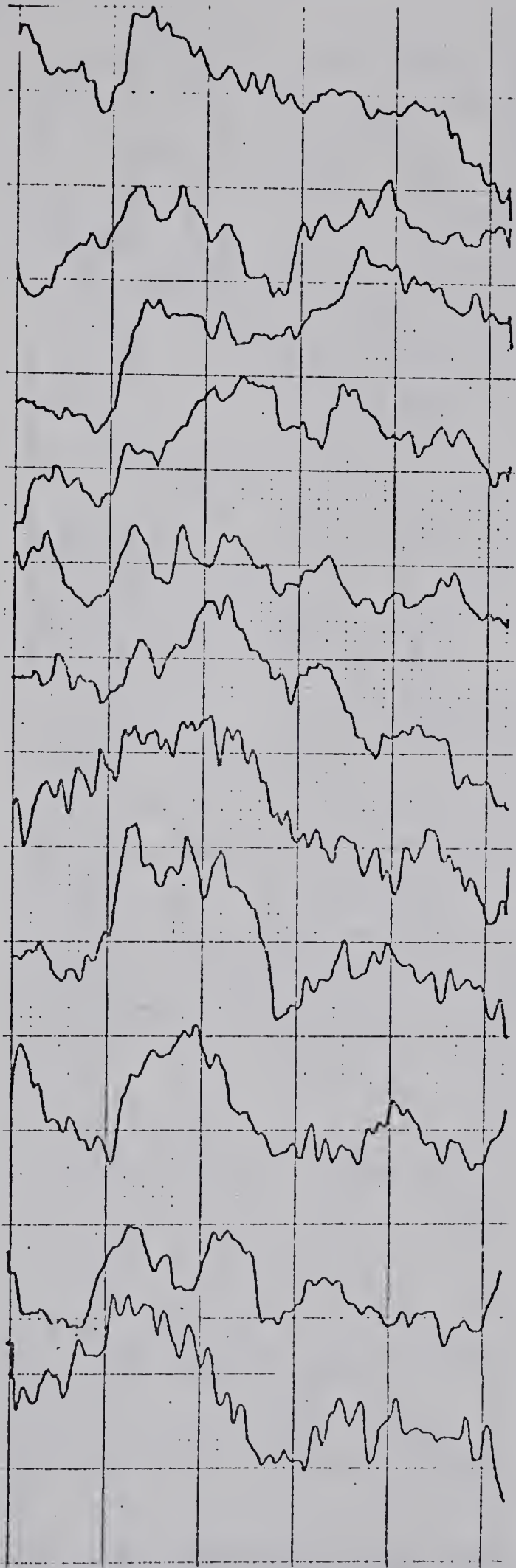
80

60

40

20

10



0 100 200 300 400 500
TIME AFTER PULSE ONSET (ms)

Fig. 5. Averaged cortical potentials evoked by various durations of a 600 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 575
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

80

60

40

20

10

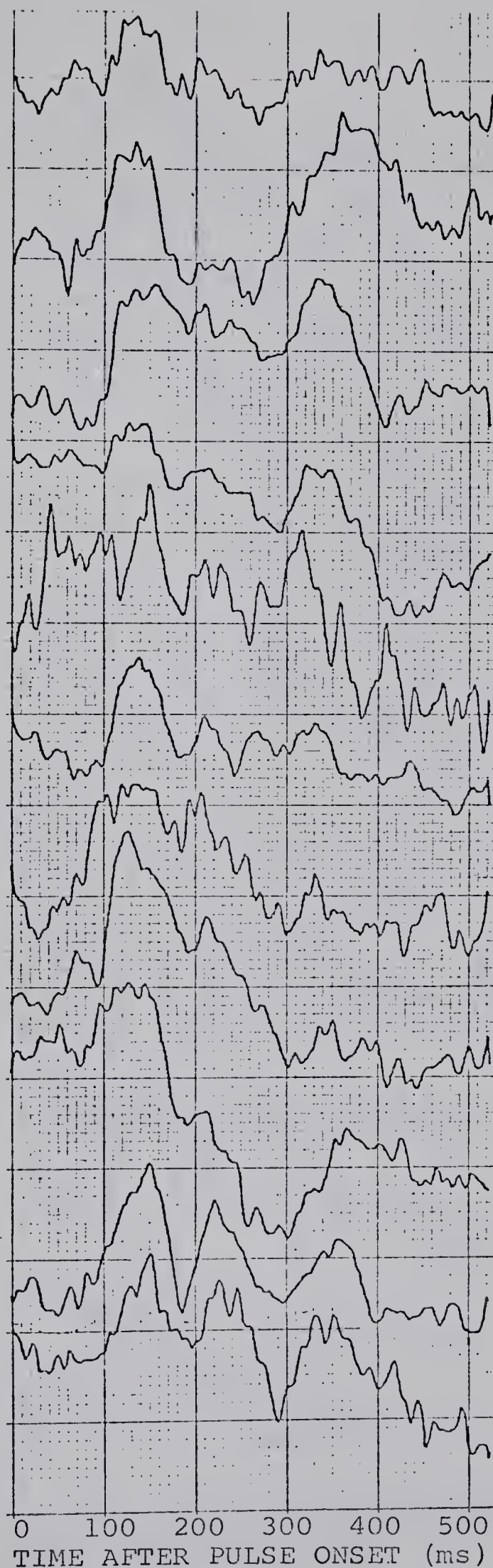


Fig. 6. Averaged cortical potentials evoked by various durations of a 575 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 550
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

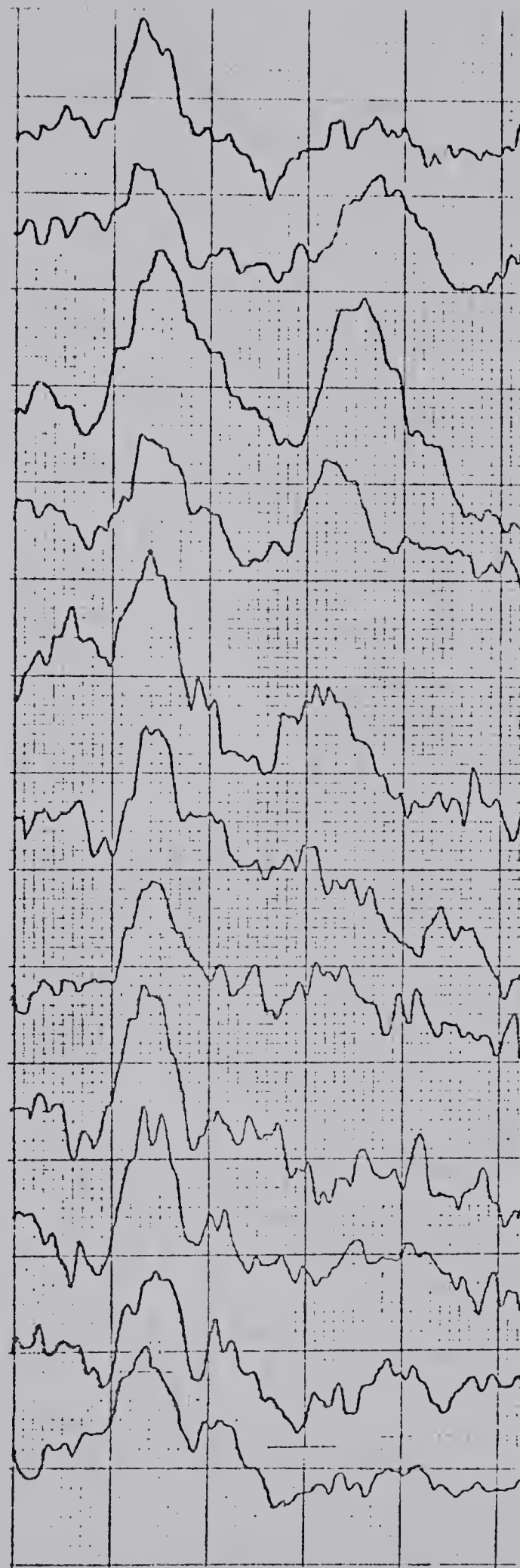
80

60

40

20

10



0 100 200 300 400 500
TIME AFTER PULSE ONSET (ms)

Fig. 7. Averaged cortical potentials evoked by various durations of a 550 nm stimulus.

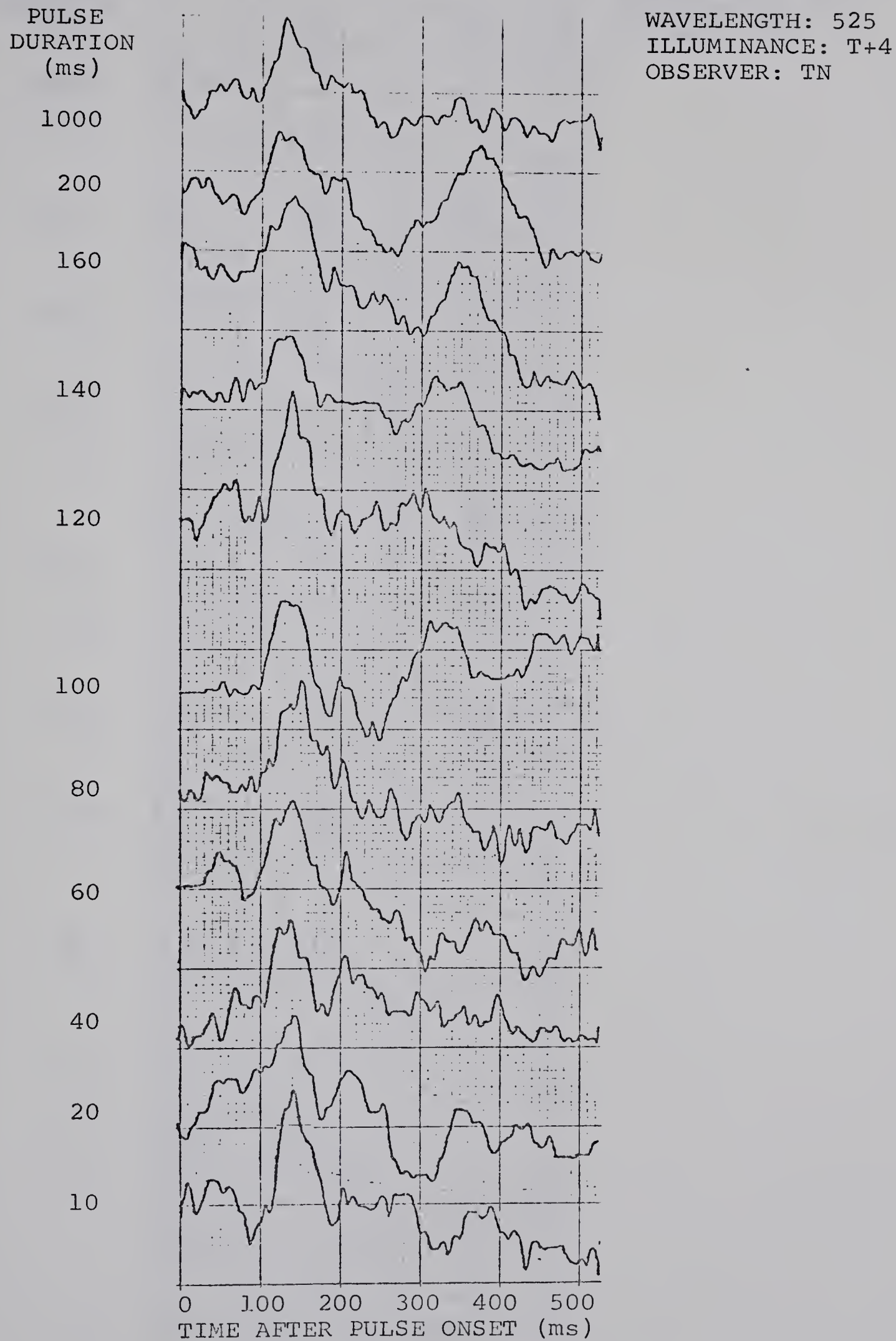


Fig. 8. Averaged cortical potentials evoked by various durations of a 525 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 500
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

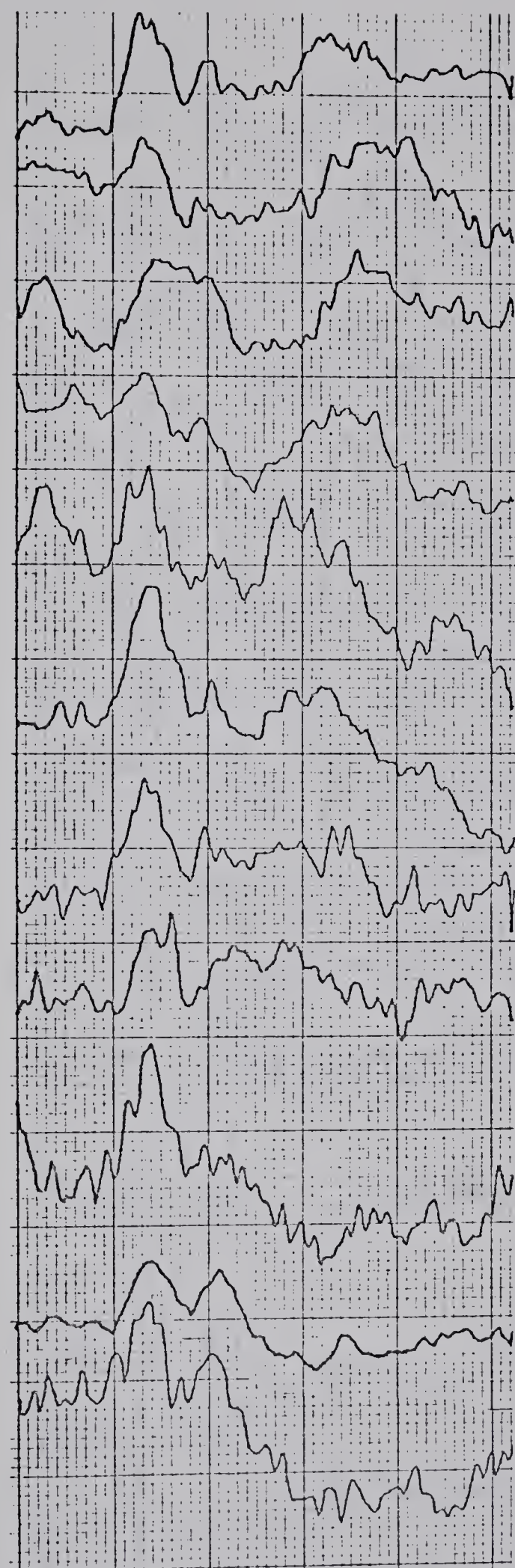
80

60

40

20

10



0 100 200 300 400 500
TIME AFTER PULSE ONSET (ms)

Fig. 9. Averaged cortical potentials evoked by various durations of a 500 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 475
ILLUMINANCE: T+4
OBSERVER: TN

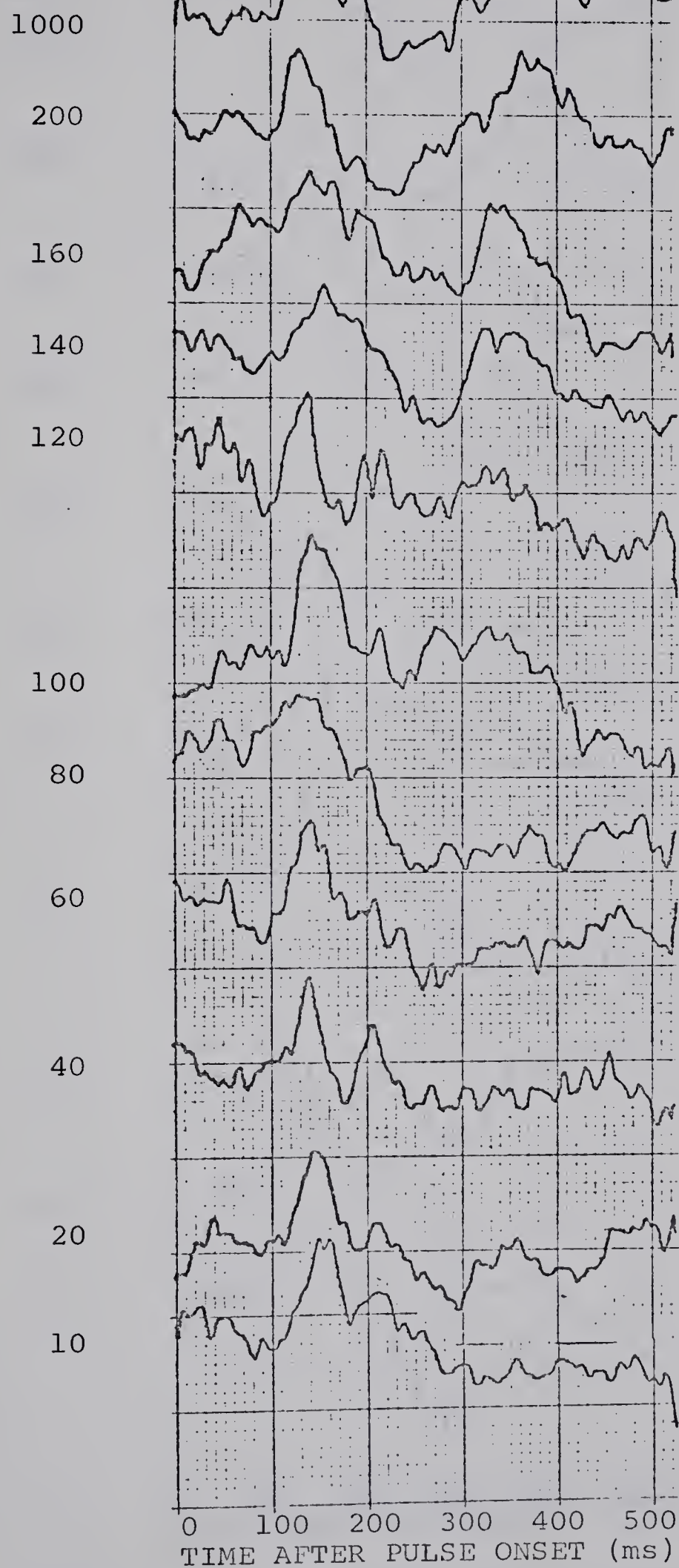


Fig.10. Averaged cortical potentials evoked by various durations of a 475 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 450
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

80

60

40

20

10

0 100 200 300 400 500
TIME AFTER PULSE ONSET (ms)

Fig.11. Averaged cortical potentials evoked by various durations of a 450 nm stimulus.

PULSE
DURATION
(ms)

WAVELENGTH: 425
ILLUMINANCE: T+4
OBSERVER: TN

1000

200

160

140

120

100

80

60

40

20

10

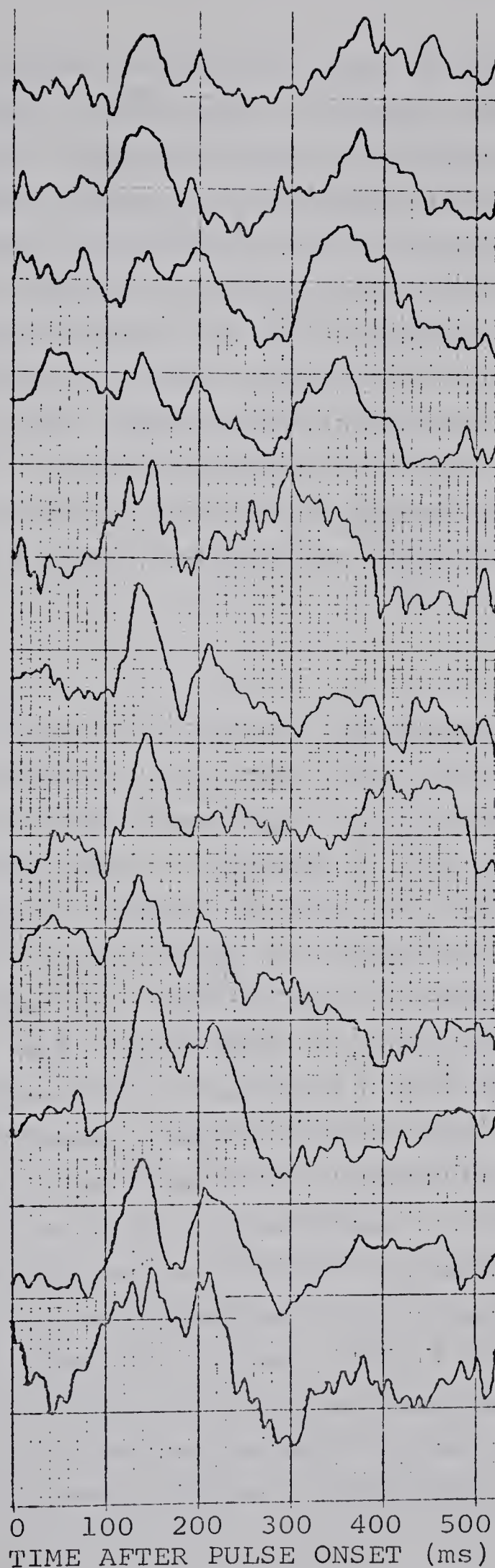


Fig. 12. Averaged cortical potentials evoked by various durations of a 425 nm stimulus.

Cortical evoked potentials were obtained by averaging the recorded EEG signals with a Digital Equipment Corporation Lab-8 computer using its Advanced Averaging Program. Evoked potential component latencies were obtained by using an adjacent point averaging program written by the author to smooth the waveform and measured using the cursor printout of the averaging program. Fourier transforms of these evoked potentials were calculated with the Lab-8 using a program written by French (1971). Crosscorrelations between evoked potentials were calculated with a Digital Equipment Corporation PDP-12 using a program written for Walter (1970).

RESULTS

Figures 1 and 2 illustrate the cortical potentials evoked in observer E.J. by 425 to 650 nm stimuli of threshold plus 2 log illuminance at 20 and 200 ms durations respectively. Figures 3 - 12 illustrate the cortical potentials evoked in observer T.N. by pulse durations from 10 to 1000 ms of threshold plus 4 log illuminance stimuli at 425 to 650 nm wavelengths respectively.

Figures 1 and 2 show that at both pulse durations E.J.'s evoked potentials followed a characteristic three peak waveform between 100 and 400 ms after stimulus onset; this was also true of his evoked potentials for the threshold plus 4 log illuminance. Figures 3 - 12 show that as either pulse duration or wavelength is varied, T.N.'s evoked potentials varied much less systematically than do E.J.'s. T.N.'s evoked potentials did not generally follow the three peak pattern of E.J.'s. E.J.'s evoked potentials bear some resemblance to those reported by Shipley, et al. (1968);

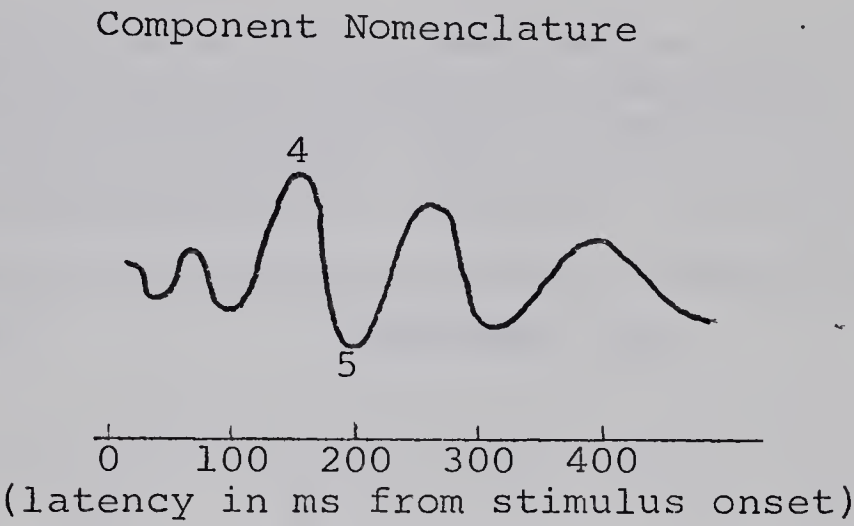
T.N.'s less so.

Decreasing pulse duration or decreasing illuminance level produced a general increase in latency of the discernable peaks in the evoked potentials of either observer. This increase in evoked potential latency with decrease in stimulus brightness has been noted previously (Wicke, et al., 1964). Other changes in waveform such as relative latencies and amplitudes of component peaks also accompanied changes in stimulus duration or illuminance level.

As stimulus wavelength is varied the latency, relative latency and relative amplitude of the component peaks again varied. The evoked potentials of E.J. do show a gradual transition in waveform with wavelength, but any transition effect is less noticeable in T.N.'s evoked potentials. Not apparent in the present data are differences in evoked potential waveform systemic with wavelength such as might permit grouping the waveforms with respect to wavelength ranges or such as simple variation in latency of a prominent peak as reported by Shipley, et al. (1968).

Table 1 shows the difference in interval between two principle waveform components in the cortical potentials from E.J. evoked by 20 and 200 ms spectral stimuli at threshold plus 2 and 4 log illuminances. This analysis sought for a relationship between the difference in hue of the 20 and 200 ms stimuli and the difference in component interval within the cortical potentials evoked by these stimuli. Differences in stimulus hue are based on the data of the present study. The analysis shows some consistency between the difference in hue and the difference in component interval when the 20 and 200 ms durations are compared at both illuminance levels for a given wavelength range. That is, when 20 ms stimuli

TABLE 1. A comparison of the difference in interval between evoked potential components 4 and 5 with the difference in hue of the 20 and 200 ms spectral stimuli.



WAVE- LENGTH	ILLUM- INANCE		INTERVAL BETWEEN COMPONENTS 4 & 5		INTERVAL DIFFERENCE (ms)	HUE DIFFERENCE (nm)
			20ms	200ms		
650	T	4 log	44	72	-28	3
625		"	76	64	12	-4.5
600		"	64	-	-	-4
575		"	76	80	-4	.5
550		"	68	60	8	6
525		"	64	60	4	8
500		"	60	68	-8	1.5
475		"	50	60	-10	-4.5
450		"	58	72	-14	-18
425		"	54	64	-10	-4.5
650	T	2 log	60	64	-4	6
625		"	80	80	0	5.5
600		"	76	88	-12	1.5
575		"	72	68	4	1.5
550		"	60	52	8	0
525		"	76	68	8	-9
500		"	68	52	16	-3.5
475		"	72	68	4	-0.5
450		"	64	68	-4	-10.5
425		"	52	60	-8	-8.5

TABLE 2. Frequencies at which power maxima occur between 3 and 20 Hz in the Fourier transforms of cortical potentials evoked from T.N. by various wavelengths of 1000, 200 and 20 ms stimuli at the threshold plus 2 (O) and 4 (X) log illuminances.

WAVE- LENGTH (Hz)	DURATION (ms)	FREQUENCY (Hz)																		
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
650	1000		⊗				⊗			⊗			○				x	○		
	200		⊗				X		○					⊗			○			
	20				X	○			X		○	X				X				
625	1000		X		○			⊗					○		X	○				
	200	⊗							X				x	○	X				○	
	20					○	X				○			X		X	○		X	
600	1000	X	○			⊗	X			○				○						
	200		⊗			⊗	○	X	○		X			X			○			
	20			X				⊗						X	○	X		X		
575	1000	○	X			⊗			⊗			X			○					
	200		⊗				⊗			X		○			○	x		○		
	20		X		○		○	X			○			X			○	X		
550	1000	○	X		○			○			X	○		○						
	200	○	X			⊗			x		○	x			○					
	20	○					X			X	○				X	○			⊗	
525	1000			○					○	X		○	X					○		
	200	X				○	X			X		○				X				
	20				⊗			○	X			X	○					X	○	
500	1000			X		○	x		○		X		○		○	x				
	200	X		○			⊗			○			X	○			○			
	20		○				○		X	○			X	○				X	○	
475	1000	○	X					○	X		X			⊗		X				
	200		X	○			X			○		X		X	○					
	20			x		○			⊗			○			X		○			
450	1000	○		○		X						○		X		x	○			
	200	X		○			X		X	○			X		○					
	20			○	X			X	○				X	○					○	
425	1000		X		○				X	○		X	○		x				○	
	200		X			⊗			○		⊗		○		○		X		○	
	20						○	X		○	X			⊗				○		
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	

TABLE 3. Some crosscorrelations between cortical potentials evoked by stimuli producing similar and different hue effects.

WAVE- LENGTH (nm)	ILLUM- INANCE (log)	DURA TION (ms)	HUE SHIFT (nm)	WAVE- LENGTH (nm)	ILLUM- INANCE (log)	DURA TION (ms)	HUE SHIFT (nm)	CROSS- CORREL ATION	HUE DIFF (nm)
525	T 4	20	8.5	525	T 4	1000	.5	.61	8
"	"	"	"	"	"	200	.5	.64	8
"	"	"	8.5	550	"	20	8.5	.79	-25
"	"	"	"	500	"	20	.5	.86	33
"	"	"	8.5	525	T 2	20	-6.5	.85	15
"	"	200	.5	525	T 4	1000	.5	.66	0
"	"	"	"	550	"	200	3	.88	-27.5
"	"	"	.5	500	"	200	.5	.02	25
"	T 2	20	-6.5	525	T 2	1000	2.5	-.10	- 9
"	"	"	"	525	"	200	1	.73	- 7.5
"	"	200	1	525	"	1000	2.5	.72	- 1.5
575	T 4	20	2.5	575	T 4	1000	.5	.44	2
"	"	"	"	"	"	200	2	.19	.5
"	"	"	"	"	T 2	20	3.5	.63	- 1.
"	"	200	2	"	T 4	1000	.5	.56	1.5
"	T 2	20	3.5	"	T 2	1000	1.5	0	2
"	"	"	"	"	"	200	2	.78	1.5
625	T 4	20	-5.	625	T 4	1000	-1.5	.68	- 3.5
"	"	"	"	"	"	200	.5	.57	- 5.5
"	"	"	"	650	"	20	4	.10	-34
"	"	"	"	600	"	20	-2.5	.58	22.5
"	"	200	.5	625	"	1000	-1.5	.19	2

from 600 to 650 nm underwent negative hue shifts with respect to the 200 ms stimuli, the interval between components 4 and 5 was always longer at both illuminance levels; when the 625 nm stimulus at the 4 log illuminance underwent a positive hue shift, the interval was shorter. However, there is a noteable exception: The 525 nm 20 ms stimuli changed in direction of hue shift with illuminance level, but both were accompanied by an increase in the component interval. Further analyses of this type were no more successful in finding a consistent relationship between change in hue and change in evoked potential waveform.

Table 2 shows the frequency components at which power maxima occurred in the Fourier transforms of cortical potentials recorded from T.N. during 1000, 200 and 20 ms stimuli of various wavelengths at the threshold plus 2 and 4 log illuminance. This analysis reveals no particular relationship between the Fourier components and the wavelength or hue shift of the stimuli.

Table 3 shows some of the crosscorrelations which were computed for various cortical potentials evoked by stimuli producing similar and different hue effects as recorded from T.N. This table shows that there is no consistent relationship between either similarity of hue or similarity of hue shift and the degree of correlation between cortical potentials evoked by stimuli producing those hue effects.

DISCUSSION

This study was undertaken to seek evidence of a temporal coding for hue as well as wavelength in the visually evoked cortical potentials. The cortical potentials evoked by spectral stimuli were found to vary with stimulus wavelength and duration. Since hue

is also affected by stimulus duration, the finding of both spectral and duration effects in cortical potentials shows that one condition for a theory of temporal coding of hue is fulfilled.

Analysis of the cortical potentials did not, however, succeed in ascertaining what characteristics are related to stimulus wavelength or perceived hue. While it is possible that a temporal code does not exist or is so complexly intertwined with a structural code to defy elucidation by purely temporal analysis, it is likely that the procedure of the present study did not permit an adequate test for a temporal code. The attempt to obtain cortical potentials evoked by 400 stimulus conditions compelled us to spread recording sessions for a single stimulus condition over several days and made it impossible to record for all stimulus conditions on any given day. While randomization of replications and stimulus conditions over days permitted reduction of systematic variance due to recording sequence, it also introduced considerable nonsystematic variance in the records.

Comparison of averaged potentials obtained on different days to the same stimulus condition revealed large differences in waveform. Some of this variability was due to differences in electrode impedance with different applications, but a more serious source of variance probably arose from an interaction between variability in electrode placement and the technique of recording the EEG. Vaughan (1969) has pointed out how differences in electrode placement result in differences in observed waveform due to the latency differences and amplitude losses during volume conduction of the responses arising at a given cortical location. Duffy (1969) has pointed out that differences in spatial orientation of the dipoles generating the

response at various locations can greatly transform the observed waveforms. With monopolar recording techniques, small differences in electrode placement might result only in small variations in absolute latency and amplitude of principle waveform components. But with the bipolar recording technique used in the present study, one is dealing with the difference between responses at each electrode at a given time, and this would seem susceptible to a much more complex variation of waveform with variation in electrode position.

Another type of variability in the evoked potential records also arose as a consequence of the attempt to sample over a large range of stimulus conditions. The sources of this type of variability are muscle artifacts and lapses of attention by the observer. Online monitoring of the EEG was performed in an attempt to catch such variability, and sessions that appeared to be noisy were stopped and repeated. However, it was at best difficult for the experimenter to monitor the EEG continuously and impossible to tell what segments were actually being recorded for evoked potential averaging. Expedition was also needed to keep observer fatigue to a minimum while recording from a large number of stimulus conditions during a given session. These facts undoubtedly contributed to variability in the evoked potential recordings within as well as across days.

The realization of the error variance introduced by the recording techniques of the present experiment suggests some steps which might be taken in future research:

- 1) A study should be made of the amount of evoked potential variability arising from small differences in electrode placement comparing monopolar and bipolar recording techniques.

2) A method permitting selective monitoring of each event related EEG signal before it is averaged could reduce trial-to-trial variability and reduce the number of trials required for nonambiguous data - an important consideration where averages must be obtained for a large number of stimulus conditions. This could be performed by storing each acquired signal in a buffer memory, displaying it as a steady waveform for 2 seconds, and giving the experimenter control over whether it is subsequently averaged with previous signals. It would seem that this could be accomplished either by a computer program or an external transient recorder.

3) It would be desirable to obtain and analyse the cortical potentials during the course of the experiment so that the results could be used either to repeat recordings or alter stimulus conditions relevant to the hue variable.

4) Finally, we may be faced with the problem that hue shifts of 10 nm may not be sufficiently large to be readily discernable by present analytic techniques even when applied to visually evoked cortical potentials obtained by optimal techniques. This suggests either that other types of analysis may be required or stimulus conditions be found which produce larger hue shifts.

One type of analysis which should be investigated is a factorial approach. A factor analysis of the temporal components within the successive EEG signals evoked by a given wavelength might prove a means of determining which components are indeed stimulus dependent. A factor analysis of the averaged cortical potentials evoked by stimuli of various wavelengths and hue would

categorize their waveforms and might thereby assist in ascertaining communalities dependent on wavelength and hue.

An attempt is being made to find stimulus conditions producing larger temporally induced hue shifts. Preliminary data on such hue shifts observed under conditions of chromatic adaptation looks promising in this regard. This experiment is described further in APPENDIX B.

APPENDIX B

Temporally Induced Hue Shifts of Monochromatic
Stimuli during Chromatic Adaptation

It has been suggested that the hue shifts induced by stimulus intermittency represent an interaction between the effects of intermittency and an intrinsic temporal code for color in the visual pathways (Nilsson & Nelson, 1971).

If hue is temporally coded within the response pattern of the color-opponent neural pathways it should be possible to alter the hue evoked by a stimulus by altering the response pattern when only a single type of color-opponent pathway is stimulated. An alternative to this postulate is that the color-opponent pathways strictly obey the law of specific nerve energies so that a single type of pathway produces only a single hue effect while hue discrimination depends on the composite responses of two or more types of pathways. The occurrence of temporally induced hue shifts does not decide the issue since different color pathways are known to have somewhat different response rise times and transmission latencies (Ingvar, 1959). But it should be possible to test these alternatives by determining if in fact hue can be changed when only a single type of color pathway is stimulated.

The technique of chromatic adaptation has been used to determine the spectral response characteristics of individual receptor pathways (DeValois, 1966). By properly choosing the wavelength of the adapting stimulus the sensitivity of one or more types of receptor pathways can be greatly reduced without unduly affecting the sensitivity of the receptor pathway under test. This technique should also permit measuring the temporally induced hue effects produced by a given type of pathway in the absence of responses by the adapted pathways to the

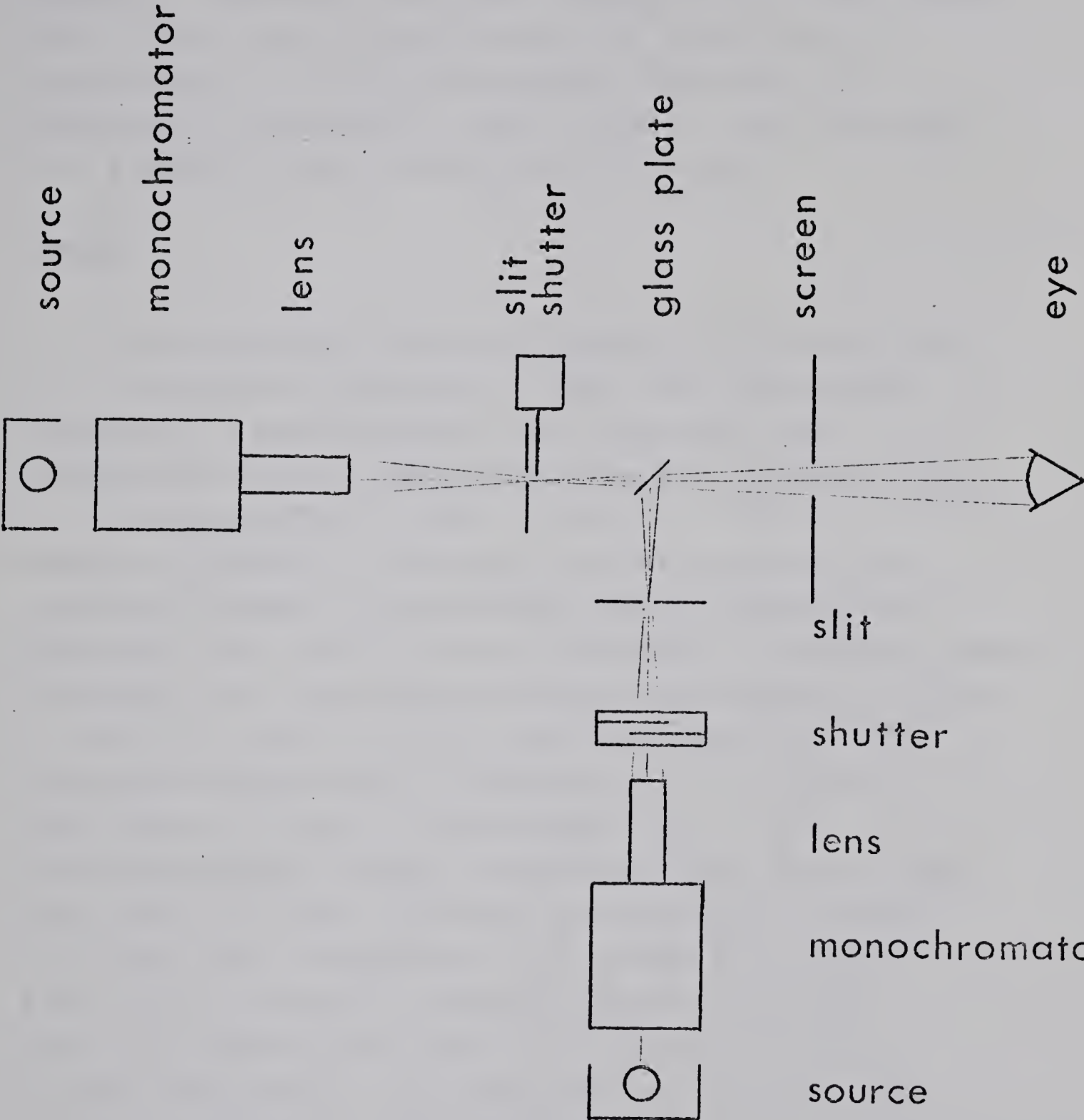
inducing stimulus.

While intermittent stimuli do not readily lend themselves to study under conditions of chromatic adaptation, the present study has shown that variations in the duration of monochromatic stimuli also results in hue shifts which are comparable to intermittency hue shifts. This finding suggests that temporally induced hue shifts can be measured under conditions of chromatic adaptation by presenting brief test stimuli of various durations alternately with relatively long presentations of the adapting stimulus.

The present study has also found that illuminance level greatly affects these temporally induced hue shifts and proposes a theory to account for these effects: At high illuminance levels, hue shifts are due to temporally enhanced activation of other opponent-color pathways in addition to those whose receptor mechanisms are being most directly stimulated by the stimulus wavelength; this results in hue shifts which are similar to Bezöld-Brücke hue shifts. At low illuminance levels, the temporal enhancement effect is restricted to pathways whose receptors are most sensitive to the stimulus wavelength, while other pathways remain inactive since at low illuminance the wavelength of the stimulus is beyond the sensitivity range of their receptors. Measuring temporal hue shifts at high and low illuminance levels under conditions of chromatic adaptation would test this theory since the theory predicts that temporally induced hue shifts could change in the direction of the hue of the adapting stimulus only at low illuminance levels.

Before building the complex apparatus required for quantitative measurements of temporal hue shifts under conditions of chromatic adaptation, it was decided to first see if any temporal hue shifts occurred at all under such stimulus conditions. We assembled an apparatus to produce just the stimulus conditions and used a

TEST - COMPARISON



ADAPTATION

Fig. 1. Schematic of apparatus used to produce the test, comparison, and adapting stimuli.

rating method to report on the observed color changes. Burnham, Onley and Witzel (1970) have shown that rating techniques can provide consistent measurements of color differences comparable to measurements obtained by other means. The following is a report of these preliminary findings.

METHOD

Two psychology graduate students, the author and A. N., served as observers. Both were experienced observers of experimental color phenomena and demonstrated normal color vision on the Ishihara test.

The apparatus is shown in Fig. 1. Two Bausch and Lomb "Hi Intensity" monochromators with tungsten filament light sources (model 33-86-25-02) were used with model 33-86-53 achromatic condenser lenses to produce the test-comparison and the adapting stimuli. 1.5 and 3 mm exit slits in the test-comparison and adapting monochromators resulted in half intensity pass bands of 5 and 10 nm respectively. An electromechanical chopper introduced into half of the beam from the test-comparison monochromator divided that beam into intermittent and steady half beams. A 2 mm slit in front of the beam chopper produced the field aperture for test and comparison stimuli in the intermittent and steady halves respectively. A thin glass plate superimposed a view of a 4 mm adaptation field aperture over the test stimulus. With a chin rest to aid maintaining eye position, the field apertures were viewed directly at a distance of 30 cm. The rectangular adjacent test and comparison stimuli each subtended visual angles of $1^{\circ}10'$ in height and $22'$ in width; the adapting stimulus was $1^{\circ}10'$ in height and $45'$ in width. These visual angles are not accurate but can serve as a guideline. Test stimulus duration was 20 ms. Adapting stimulus duration was 3 sec, produced by a Lafayette

Instruments model V51-E shutter. Duration and temporal frequency of the test and adapting stimuli were controlled by a series of transistorized timers (Nilsson, 1969). Onset of the test stimulus followed offset of the adapting stimulus after a 500 msec delay; onset of the adapting stimulus followed offset of the test stimulus after a 1 sec delay. Illuminance of the stimuli was not calibrated or equated across wavelengths, but at full illuminance the stimuli were approximately 5 log above photopic threshold at 575 nm, approximately 4 log above threshold at 650 nm, and 3 log above threshold at 425 nm. Illuminance of the test and comparison stimuli was varied by adding Tiffen neutral density filters; the adapting stimulus was always at full illuminance.

Ten test-comparison stimulus wavelengths were used ranging from 425 to 650 nm. Three test-comparison stimuli illuminance levels of full illuminance, -2 log, and -3 or -4 log were used. (Adapting stimuli between 500 and 600 nm were generally too bright to permit color judgements of test-comparison stimuli at -4 log; illuminance of test-comparison stimuli was then raised to -3 log.) Six adapting stimulus wavelengths of 420, 450, 500, 535, 578, and 635 nm were used. These values were chosen to approximate the peak sensitivity of the three types of spectral receptors and the four types of color-opponent pathways based on reports by Marks, et al. (1964) and DeValois (1966) respectively. For a given adapting wavelength, observations were made successively at each experimental wavelength. Experimenter and observer traded roles after conditions for two adapting wavelengths had been observed.

A psychophysical rating method was used to measure the hue change and saturation change of the test stimulus, which had been preceded by an adapting stimulus, relative to the steady comparison stimulus. Both attributes

TABLE 1: Estimates of hue shift of the 20 ms test stimulus relative to the comparison stimulus as function of test-comparison and adapting wavelength and as function of illuminance of test-comparison stimulus.

TEST (nm)	ILLUM. (log density)	ADAPTING WAVELENGTH (nm)											
		420		450		500		535		578		635	
		AN	TN	AN	TN	AN	TN	AN	TN	AN	TN	AN	TN
425	0	- $\frac{1}{2}$	0	0	2	-2	0	-1	-3	-3	-2	0	0
	-2	0	0	1	0	1	-3	-3	-3	-2	-3	-4	-4
450	0	0	0	- $\frac{1}{2}$	0	-2	0	-2	-2	-3	-2	0	0
	-2	1	1	0	0	-1	-2	-3	-2	-3	-3	-4	-4
475	0	0	0	4	0	-1	-1	-2	-2	-2	-1	0	-1
	-2	1	3	5	-	-1	-2	-1	-3	-3	-3	-3	-2
	(-3)-4	-2	-3	-3	-2	-1		(-2)		(-2)(-3)		-3	-3
500	0	1	3	3	4	0	0	-3	-2	-3	-3	-3	-2
	-2	2	3	4	1	3	0	-4	-3	-4	-4	-3	-1
	(-3)-4	-4	-4	-3	-3	3		(-2)		(-2)(-3)		-3	-3
525	0	1	2	$\frac{1}{2}$	2	1	4	-1	-1	-4	-4	-4	-4
	-2	3	4	3	4	4	1	3	1	-4	-4	-4	-2
	(-3)-4	-1	-2	4	-4	1	-1	(-4)(0)		(-4)(-4)		-4	-4
550	0	0	1	0	3	1	3	0	1	0	0	0	-4
	-2	1	4	3	4	3	4	2	2	-4	-1	-4	-2
	(-3)-4	1	1	2	4	2	0	(1)(0)		(-4)(-3)		-4	-4
575	0	-1	2	0	3	1	3	2	3	1	1	0	-4
	-2	2	3	1	3	0	2	0	-1	0	0	-2	-3
	(-3)-4	2	3	3	3	0	0	(0)(0)		(0)(0)		-5	-5
600	0	0	1	-1	4	0	3	2	3	1	1	-3	-3
	-2	1	2	2	2	-2	0	-1	-1	0	1	0	0
	(-3)-4	1	3	2	3	-1	-1	(2)(-3)		(0)(0)		-4	-5
625	0	2	2	-2	3	-1	1	-1	1	1	2	-3	0
	-2	2	2	1	2	-3	1	-3	-2	2	0	2	1
	(-3)-4	-4	- $\frac{1}{2}$	0	-1	-1	-1	-2(2)		(-2)(0)		(0)(0)	
650	0	2	2	-1	2	-1	1	-1	-2	1	1	-4	0
	-2	1	1	1	2	-3	1	-2	-2	2	-2	3	2
	(-3)	(- $\frac{1}{2}$)(1)		(-1)(1)				(2)			-2		0

were rated on a 0 to 4 scale; 0 represented no change in either hue or saturation. On the hue scale, 4 represented a complete change from one primary hue to an adjacent primary hue, such as mid green to mid yellow; positive or negative values indicated if the hue change was in the direction of hues normally produced by longer or shorter wavelengths. On the saturation scale, -4 represented complete desaturation; positive values became necessary to represent a supersaturation which might best be described as the test stimulus being brighter than the comparison stimulus but not desaturated.

RESULTS

Table 1 shows estimates of hue shift of the test stimulus relative to the comparison stimulus as a function of test-comparison and adapting stimulus wavelengths. The results show that magnitude and direction of hue shift varied with test stimulus wavelength, adapting stimulus wavelength, and illuminance. There appears to be no trend in hue shift magnitude as a general function of either test stimulus or adapting stimulus wavelength. Depending on other conditions all wavelengths were accompanied by both large and negligible hue shifts. Direction of hue shift predominantly varied so that the test stimulus shifts in a direction opposite to the wavelength of the adapting stimulus. But at the lower illuminance levels there were exceptions to this contrast effect:

- 1) 475 and 500 nm test stimuli underwent negative hue shifts when the adapting wavelength is shorter.
- 2) The 525 nm test stimulus underwent a negative hue shift with 420 and 450 nm adapting wavelengths. There is some ambiguity between the observers on this point, but subsequent reports by other observers confirm this effect.
- 3) The 600, 625, and 650 nm test stimuli shifted.

TABLE 2. Estimates of saturation changes of 20 ms test stimulus relative to comparison stimulus as function of test-comparison and adapting wavelength and as function of illuminance of test-comparison stimulus.

TEST (nm)	ILLUM. (log density)	ADAPTING WAVELENGTH (nm)											
		420		450		500		535		578		635	
		AN	TN	AN	TN	AN	TN	AN	TN	AN	TN	AN	TN
425	0	-1	-2	-4	-3	2	-3	-1	1	-2	0	0	0
	-2	-2	$\frac{1}{2}$	-1	1	-2	1	2	2	1	0	0	1
450	0	-3	-1	$-3\frac{1}{2}$	-4	0	-3	-3	0	-2	0	0	0
	-2	0	1	-2	1	-1	1	2	2	0	1	-1	0
475	0	-3	-3	-3	-3	-2	-3	0	0	-3	-1	0	0
	-2	0	0	-3	-2	$-\frac{1}{2}$	0	1	2	-1	0	-1	0
	(-3)-4	0	0	-2	-3	-1		(-1)				-1	
500	0	0	-1	-2	0	-4	-4	-3	0	-3	0	-2	0
	-2	-1	-3	-3	-4	-2	-4	-2	1	-1	0	-2	-1
	(-3)-4	0	0	-2	0	0		(-1)		(-2)	0	-2	0
525	0	-2	-1	-2	0	2	0	-3	-3	-3	0	-3	0
	-2	-1	-2	0	-2	0	-3	-2	-3	-2	-1	-3	-3
	(-3)-4	0	0	-2	-2	-1	-2	(-3)	(-4)	-2	0	-2	0
550	0	-1	0	-1	0	0	0	-2	-3	-4	-4	-4	0
	-2	1	-1	-1	0	0	0	0	0	-3	-4	-3	-3
	(-3)-4	-1	-3	0	-3	0	-3	(-1)	(-4)	(-3)	(-3)	-2	-1
575	0	$-\frac{1}{2}$	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	1	-1	0	-3	-4	0
	-2	1	0	1	-1	0	0	-1	-2	-3	-2	-1	0
	(-3)-4	-2	0	1	1	0	0	(-2)	(-4)	(-3)	-4	-2	-3
600	0	-1	0	0	0	0	0	0	0	0	-2	-3	-3
	-2	0	0	2	0	-1	0	-2	0	-2	-2	-3	-4
	(-3)-4	0	0	1	1	-1	-1	(-2)	(-2)	(-1)	(-3)	-4	-3
625	0	1	0	-1	2	-1	0	-2	0	1	-2	-2	-3
	-2	2	1	1	1	-2	0	-3	-2	-2	-2	-2	-3
	(-3)-4	0	0	-1	-1	0	-2	(-2)	(-1)	(-2)	(-3)	(-3)	(-3)
650	0	1	0	-2	1	-2	0	-2	0	-2	-2	-3	-3
	-2	1	1	0	1	-3	1	-3	-3	-3	-3	-1	-3
	(-3)	(0)	(0)	(-1)	(0)			(-2)			-2		0

negatively with 500 and 535 nm adapting wavelengths.

Table 2 shows estimates of saturation changes of the test stimulus relative to the comparison stimulus as a function of test-comparison and adapting wavelengths. The only discernable trend in these results is that desaturation was greatest when test and adapting wavelengths are similar.

DISCUSSION

The finding that desaturation of the test stimulus is greatest when the adapting stimulus is of a similar wavelength seems in accord with Walraven's (1961) theory of the Bezöld-Brücke effect and the paradigm for temporal hue shifts presented in the main part of this report. Given that the adapting stimulus has desensitized that type of receptor generally responding to the test stimulus, the effect of the test stimulus will depend considerably on its ability to excite the other types of receptors - the result is then a response similar to the response which would normally be produced by a very broad pass band stimulus.

Examination of Table 1 shows numerous instances where hue shifts are reported to have magnitudes of 3 and 4. On the basis of the scale criteria, this would correspond to hue shifts of 25 to 50 nm and more. Such hue shifts are considerably larger than any previously measured temporal hue shifts. The fact that such magnitudes occur contrary to the color adaptation effect suggests that these would be suitable conditions under which to study cortical potentials evoked by inducing temporal hue shifts in an attempt to find characteristics invariant with hue as opposed to wavelength.

The finding that hue shifts are generally in a direction opposite to that of the adapting wavelength is simply a

manifestation of the well known color adaptation effect (Graham & Brown, 1965). What is of particular interest in the present results is the discovery that hue shifts can occur contrary to this color adaptation effect. Since these occur only at the lower illuminance levels of the test stimulus, they can not be due to ineffectiveness of the adapting stimulus. The observed hue shifts can therefore not be due to the test stimulus managing to excite additional receptor types. Rather, in accord with the proposed paradigm for temporal hue shifts, this demonstrates that the change in hue is the result of response changes in the given color pathway excited by the test stimulus wavelength. This then is further evidence that variations of hue are coded within color pathways. The all-or-none law demands that such a code be of a temporal nature.

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